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Part A. Supplementary Notes

1) Geological Provenance and Stratigraphy

The specimens described in this paper (GIT 496-6 [Pi.1384]; GIT 496-7 [Pi.1383]; Extended Data Figure 1) are from the lower member of the Kureika Formation on the Sida River, Kotui Basin, Siberia (Schultze 1992). The Kureika Formation, part of the North-Western Siberian Platform, is clearly Early Devonian in age. Early stratigraphic assessments correlated the Kureika Formation with the Siegenian (Pragian-Emsian; Krylova et al. 1967) or Gidennian-Siegenian (Early Devonian; Obruchev, 1973). More recent efforts have indicated a Lochkovian age (e.g., Cherksova 1988). This assessment is supported by the presence of *Rhinopteraspis* from the Norilsk outcrop of the upper part of the Kureika Formation, first described by Obruchev (1964, pl. 2: fig. 4). This specimen was identified as most likely belonging to *Rhinopteraspis crouchi*, although the possibility of it being a juvenile *R. dunensis* has been raised (Blieck 1984, Blieck and Janvier 1993). If the specimen belongs to *R. crouchi*, this would date the upper part of the Kureika Formation to the middle Lochkovian (ca. 415Ma; Gradstein et al. 2012); if *R. dunensis*, it would indicate a Pragian age (Blieck 1984). Other palaeontological evidence from lateral equivalents of the Kureika Formation is consistent with a Lochkovian age. The Bely Kamen (or Belokamensk) beds from the central Taymir are interpreted as the lateral equivalent of the lower unit of the Kureika Formation that yields material of *Janusiscus* (Novitskaya 1977). A diverse fauna of amphiaspids, including *Tareyaspsis*, *Gunaspsis*, *Agyriaspsis* and *Prosarctaspsis*, along with acanthothoracid placoderms, the acanthodians *Gomphonchus*, *Nostolepis*, *Cheiracanthoides* and *Taimyrolepis*, and the sarcopterygian *Porolepis* have been reported from the Bely Kamen beds (Karatajute-Talimaa 1994; Valiukevicius 1994). The overlying Uryum beds are correlated with the middle member of the Kureika Formation (Novitskaya 1977), and yield the heterostracans *Rhinopteraspis*, *Tareyaspsis*, *Gabreyaspsis*, *Agyriaspsis*, *Empedaspsis*, *Pelaspsis*, *Siberiaspsis* and *Norilaspsis*, placoderms including *Romundina*, *Palaeacanthaspsis*, and indeterminate acanthothoracids and palaeacanthaspsids, the acanthodians *Gomphonchus*, *Nostolepis*, *Poracanthodes*, *Cheiracanthoides*, *Taimyrolepis* material doubtfully attributed to ?*Acanthodes*, and the sarcopterygian *Porolepis* (Karatajute-Talimaa 1994; Mark-Kurik 1994; Valiukevicius 1994). In light of these faunal data, we are confident that the deposits yielding *Janusiscus* are Lochkovian in age, and probably date to the early part of that stage.

The Siberian Platform is a lagoonal marine shelf deposit, with the north-western section of the platform, in which the Kureika Formation is located, deposited in a shallow water environment (Cherksova 1988). Although limited stratigraphical information is associated with the site where the fossil was found, the lower part of the Kureika formation at other locations is deposited as a succession of grey argillites with interbedded limestones and clay-rich dolomites (Novitskaya 1977).

2) Taxonomic Notes and History

The type species of *Dialipina*. The type species of *Dialipina*, *D. salgueiroensis*, was erected for scales and a dermal bone fragment found in the Early Devonian (Emsian) Bear Rock Formation (?Delorme Formation) of northwest Canada (Schultze 1968). The holotype of *D. salgueiroensis* is a scale bearing a prominent, but broken, dorsal peg and

ornamented with ridges of enamel (Schultze 1968: fig. 7; Extended Data Figure 2d). Schultze (1968) diagnosed *Dialipina* on the basis of features of scale ornament: principal enamel ridges that extend parallel to the anterior margin of the scale anteriorly, but extending parallel to the ventral margin of the scale posteriorly; fine transverse striations on the vertically oriented anterior portions of the principal enamel ridges; posterior serration of the scale produced by short enamel ridges intercalated between the principal enamel ridges. Articulated specimens assigned to this species have since been described from this locality (Schultze and Cumbaa 2001).

Referred species of *Dialipina*. Mark-Kurik (1974) described scales from the 'Gedinnian' (Early Devonian: Lochkovian) of the New Siberian Islands, Russia, and noted their morphological similarity to *Dialipina salgueiroensis* (Extended Data Figure 2e). Schultze (1977: figs 3a-g, 4a-b; pl. 14) provided a more detailed account of these scales. A more detailed description by Schultze (1977: figs 3a-g, 4a-b; pl. 14) found conspicuous differences between these scales and those of the Emsian *D. salgueiroensis*: (i) enamel ridges straight (rather than bent anteriorly as in *D. salgueiroensis*); (ii) enamel ridges smooth (*versus* ornamented with fine transverse striations as in *D. salgueiroensis*); (iii) irregular patterning of short enamel ridges intercalated between principal enamel ridges (*versus* highly regular packing pattern of these short intercalating ridges in *D. salgueiroensis*); (iv) low rounded dorsal peg and small anterodorsal process (*versus* high, pointed dorsal peg and well-developed anterodorsal process in *D. salgueiroensis*); (v) presence of cell-spaces basal bone of scales (*versus* no cell-spaces in *D. salgueiroensis*); (vi) scale bases with two layers of highly vascularized, cancellous bone bearing cell spaces (*versus* lamellar bone without lacking cell spaces and bearing non-vascular canals of Williamson). Despite these prominent differences, Schultze (1977) considered these Lochkovian scales congeneric with *D. salgueiroensis*, and erected the new species *D. markae* to accommodate them.

We regard evidence for placement of these morphologically and histologically different scales in the same genus as suspect. *D. salgueiroensis* bears scales with peg-and-socket articulations, a synapomorphy of osteichthyans crownward of *Andreolepis*, *Naxilepis*, *Orvikuina*, and *Terenolepis* (Friedman and Brazeau 2010). With their rudimentary dorsal pegs that are little more than elaborated overlap areas, the scales of *D. markae* broadly resemble those assigned to the stem osteichthyans *Andreolepis* and *Orvikuina*. We suggest that *D. markae* likely falls outside the clade *D. salgueiroensis* + crown Osteichthyes.

Identification of fossil fish remains from the Kureika Formation. The cranial remains described here are from two localities of the lower member of the Early Devonian (Lochkovian) Kureika Formation along the Sida River in Siberia. These fossils were first reported by Schultze (1992), who attributed them to *Dialipina markae*. This assignment is based on the presence of scales in the same deposit that Schultze (1992) identified as belonging to *D. markae* (Table 1; Extended Data Figures 2a-c,f,g). The attribution of the skull roofs to *D. markae* is therefore predicated on two assertions: that the scales from the lower member of the Kureika Formation clearly belong to *D. markae*, and that the skull roofs can then be positively linked with these scales. We find both claims questionable.

Schultze (1992) attributed scales from the Kureika Formation to *D. markae* based on the presence of parallel ridges of ornament separated by grooves and absence of a large dorsal articular peg. Both features are widely distributed among gnathostomes, and are therefore of doubtful value in specific assignments. Furthermore, Schultze (1992: p. 236) noted features in which the scales from the Kureika Formation differed from those of *D. markae*, found in a different formation some 1500 km away. Most significantly, the attributed scales from the Kureika Formation rarely show short ridges of ornament that intercalate between principal ridges at the posterior of the scale. The presence of such intercalating ridges, resulting in a serrated posterior margin of the scale, is the principal feature hypothesized to unite both species of *Dialipina* (Schultze 1977: fig. 1, 'a.g'; Extended Data Figure 2d-e). Such pronounced serration is not apparent in scales from the lower member of the Kureika Formation that show clear outlines or impression of the posterior margin (GIT 496-5, 496-8, 496-10; Extended Data Figure 2a,b), contradicting attribution to *D. markae*. A single scale from the lower member of the Kureika Formation does bear clear serration (GIT 496-16; Extended Data Figure 2c), but this specimen was highlighted by Schultze (1992) as bearing ridges that curve anteriorly so as to parallel the anterior margin of the scale. This feature is inconsistent with attribution to *D. markae*. Such ornament is present in *D. salgueiroensis*, however, and was considered an important feature distinguishing this species from *D. markae* (Schultze 1977).

Specimen number in Schultze (1992)	New specimen number	Outcrop	Description	Schultze (1992) attribution
Pi 1381	GIT 496-4	C-2	?cleithrum (inner surface exposed)	? <i>Dialipina</i>
Pi 1382	GIT 496-5	C-2	rhombic scale (worn, showing ornament ridges and impression of external surface)	<i>Dialipina markae</i>
Pi 1383	GIT 496-6	C-27	skull roof and braincase	<i>Dialipina markae</i>
Pi 1384	GIT 496-7	C-15	skull roof	<i>Dialipina markae</i>
Pi 1384a	GIT 496-8	C-15	rhombic scale (external surface exposed)	<i>Dialipina markae</i>
Pi 1384b	GIT 496-9	C-15	rhombic scale (external surface exposed with broken posterior half, revealing ornament on external face)	<i>Dialipina markae</i>
Pi 1385a	GIT 496-10	C-24	rhombic scale (internal surface exposed)	<i>Dialipina markae</i>
Pi 1385b	GIT 496-11	C-24	rhombic scale (internal surface exposed)	<i>Dialipina markae</i>
Pi 1385c	GIT 496-12	C-24	indeterminate	<i>Dialipina markae</i>
Pi 1386a	GIT 496-13	C-24	rhombic scale (external surface exposed)	<i>Dialipina markae</i>
Pi 1386b	GIT 496-14	C-24	rhombic scale (external surface exposed)	<i>Dialipina markae</i>
Pi 1386c	GIT 496-15	C-24	rhombic scale (external surface exposed)	<i>Dialipina markae</i>
Pi 1387	GIT 496-16	C-15	rhombic scale (external surface exposed)	<i>Dialipina</i> sp.

Table 1| Fish remains from the lower member of the Early Devonian Kureika Formation, Sida River localities, Siberia previously attributed to *Dialipina*.

In addition to contrasting ornamentation indicated by Schultze (1992) between scales from the Kureika Formation and those of *D. markae*, we note additional differences in overall scale geometry. Scales of *D. markae* figured by Schultze (1977: fig. 1a-g, pl. 14) bear well-defined dorsal pegs that range in shape from humped (fig. 1b) to triangular

(fig. 1g). By contrast, the rudimentary dorsal pegs in specimens from the Kureika Formation are developed as low, broad flanges, and are less prominent than those of *D. markae* (Extended Data Figures 2a-c,f,g). In light of these clear differences, we argue that neither scale morphotype (scales with linear ridges and lacking posterior serration; scales with curved ridges and bearing posterior serration) can be reliably attributed to *D. markae* on the basis of morphology. This would seem consistent with the fact that the sites bearing these scales are remote from the type locality of *D. markae*, which yields an Early Devonian fauna considered biogeographically distinct from that of the northwestern Siberian Platform (Blicek and Janvier 1993: 99).

Although we regard the specific attribution of scales to *Dialipina markae* dubious in any case, it is important to review the evidence suggested to link these fossils with co-occurring cranial remains. We do not accept arguments that derivation from the same geological unit is sufficient evidence to unite disarticulated remains within a single taxon. Concerning morphological evidence for attribution of the skull roofs to the scales, Schultze (1992: 236) only notes that the cranial remains “are covered by longitudinal smooth ridges similar to the ornamentation on scales of *D. markae*.” Longitudinal ornament ridges are widely distributed feature of early gnathostomes, and as such their presence on both scales and skull bones from the Kureika Formation represents weak evidence for their attribution to a single species.

In light of the tenuous chain of attributions linking skull roofs GIT 496-6 (Pi1383) and 496-7 (Pi1384) to type material of *Dialipina markae*, we conclude that the most responsible taxonomic act is to erect a new species to accommodate these specimens. Even if subsequent collection provides unambiguous evidence for association of the rhombic scales from the Kureika Formation with these skull roofs (i.e., articulated or associated fossil specimens), we regard the differences apparent between these scales and descriptions provided for *D. markae* sufficient to merit species-level distinction. Should articulated or associated remains show that these different scale morphotypes are present within single individuals, and that some scales more precisely match those of *D. markae*, then we note that *Janusiscus schultzei* could be reassessed as junior synonym of that species. However, that species could not be assigned to *Dialipina*, given the profound differences in cranial and scale anatomy noted here (Extended Data Figures 1,2), and *Janusiscus* would be available to accommodate it.

Comparison of skull roofs from the Kureika Formation with *Dialipina*. Our reexamination of these fossils has resulted in a new interpretation of dermal bone patterns in GIT 496-6 (Pi1383) relative to that given by Schultze (1992: fig. 5). He considered this specimen the anterior half of a skull roof, but its position relative to the underlying braincase clearly indicates it is the posterior half of a skull roof. The large paired bones represent postparietals, rather than parietals, and the bone previously interpreted as the pineal can now be identified as the parietals (Extended Data Figure 1). Regions described as impressions of different dermal bones are now identified as portions of the underlying braincase. This reinterpretation brings the anatomy of GIT 496-6 (Pi1383) in line with that of GIT 496-7 (Pi1384).

The ornamentation and proportions of the skull roofs from the Kureika Formation differ significantly from *Dialipina salgueiroensis* (Extended Data Fig. 1). Most notably, the Siberian specimens lack the anterolateral extensions seen on the parietals of *D.*

salgueiroensis. Other major differences apparent in the Siberian skulls include: strongly concave posterior margins of the parietals (*versus* slightly convex in *D. salgueiroensis*); postparietals larger than parietals (*versus* parietals larger than postparietals in *D. salgueiroensis*); pineal plate narrow (*versus* a broad pineal plate in *D. salgueiroensis*); skull roofing bones ornamented with broad ridges that can extend the length of individual ossifications (*versus* narrow, short ornament ridges in *D. salgueiroensis*).

3) Lateral Processes of Early Gnathostome Neurocrania

Taxon	Studies	Postorbital process	Transverse otic process	Vagal process(es)	Craniospinal process
Sarcopterygii	Jarvik (1980)	Suprapterygoid process	Lateral commissure	n/a	n/a
	Yu (1998) Zhu and Yu (2002) Zhu et al. (2013)	Postorbital pila (in part)	Lateral commissure	n/a	n/a
Actinopterygii	Rayner (1951) Jarvik (1980) Gardiner (1984)	Postorbital process	Lateral commissure (in part)	n/a	Craniospinal process
	Zhu et al. (2013)	Lateral commissure (in part)	Lateral commissure (in part)	n/a	n/a
Ligulalepis	Basden et al. (2000) Basden and Young (2001)	Postorbital process	Unnamed	n/a	n/a
	Zhu et al. (2013)	Lateral commissure (in part)	Lateral commissure (in part)	n/a	n/a
Chondrichthyes	Jarvik (1980) Maisey (2005)	Postorbital process	n/a	n/a	n/a
	Schaeffer (1981) Coates and Sequeira (1998)	Postorbital process	Lateral otic process	n/a	n/a
Acanthodes	Miles (1973) Jarvik (1980)	Postorbital process	Unnamed	n/a	n/a
	Davis et al. (2012)	Postorbital process	Unnamed	n/a	n/a
Ramirosuarezia	Pradel et al. (2009)	Pr1	Lateral commissure + Pr3	n/a	n/a
Entelognathus	Zhu et al. (2013)	Postorbital pila	Anterior postorbital process	Posterior postorbital process	Craniospinal process
Dicksonosteus	Young (1980)	Supraorbital process	Anterior postorbital process	Posterior postorbital process + supravagal process	Craniospinal process
	Goujet (1984)	Unnamed	Anterior postorbital process	Posterior postorbital process	Craniospinal process
Kujdanowiaspis	Stensiö (1969) Jarvik (1980)	Supraorbital process	Anterior postorbital process	Posterior postorbital process	Supravagal process
	Goujet (1984)	Supraorbital process	Anterior postorbital process	Posterior postorbital process	Craniospinal process
Buchanosteus	Young (1979) Young (1980)	Supraorbital process	Anterior postorbital process	Posterior postorbital process	Craniospinal process
Jagorina	Stensiö (1969)	Supraorbital process	Anterior postorbital process	Unnamed	Supravagal process
	Jarvik (1980)	Unnamed	Unnamed	Unnamed	Supravagal process
	Young (1980)	Supraorbital process	Unnamed	Posterior postorbital process	Supravagal process
Romundina	Ørvig (1975)	n/a	Anterior postorbital process	Posterior postorbital process	Supravagal process
	Young (1980)	n/a	Anterior postorbital process	Posterior postorbital process + craniospinal process	Supravagal process
Macropetalichthys	Stensiö (1969)	n/a	Anterior	Supravagal	Craniospinal

			postorbital process + posterior postorbital process	process	process
	Jarvik (1980)	n/a	Unnamed	Supravagal process	Craniospinal process
	Young (1980)	n/a	Anterior postorbital process	Posterior postorbital process + supravagal process	Craniospinal process
<i>Brindabellaspis</i>	Young (1980)	n/a	n/a	Infravagal process + supravagal process + postglossopharyngeal ridge	Craniospinal process
<i>Osteostraci</i>	Janvier (1985)	n/a	n/a	Prebranchial ridge	n/a

Table 2| Terminology applied to lateral neurocranial processes in early vertebrates in this and previous studies.

The braincases of early gnathostomes bear a diversity of lateral processes showing variable relationships with other neurocranial landmarks like foramina for cranial nerves and circulatory vessels. These processes have attracted a range of descriptive terms, with many names being applied specifically to certain taxonomic assemblages (e.g., ‘placoderms’). Unfortunately, these parallel schemes of nomenclature have hindered more direct comparisons between the character-rich braincases of early gnathostomes. The most extensive effort to rationalize naming systems in early gnathostomes was provided by Young (1980:54-61), who sought to standardize terminology across ‘placoderms’. We have drawn heavily on his arguments concerning processes present posterior to the articulation of the hyoid arch (features variously termed posterior postorbital, vagal, supravagal, and craniospinal processes), with minor exceptions mentioned specifically below. The significance of *Janusiscus* to this nomenclatural problem is the conjunction of braincase structures that allow us to propose homologies between processes found in both crown gnathostomes and ‘placoderms’, but which have traditionally been referred to using assemblage-specific terminology.

Postorbital process: a dorsally placed process that forms the rear margin of the orbital region. It may be pierced or notched by the jugular canal or imperforate. This structure has generally been referred to as the supraorbital process in ‘placoderms’ (e.g., Young 1980: fig. 24). The ‘placoderm’ postorbital process defines the posterodorsal boundary of the orbit, and as such corresponds positionally to the primary postorbital process (*sensu* Holmgren 1940: fig. 67) of modern elasmobranchs. ‘Placoderms’ lack a ventral bridge extending from the postorbital process that encloses the jugular vein against the neurocranial wall, but such a commissure is some chondrichthyans and sarcopterygians. Here we refer to the entire postorbital extension, which may or may not include a lateral commissure, as the postorbital process.

Presence or absence of a postorbital process is recorded by character 132. The presence of a jugular canal in the postorbital process (i.e., enclosure formed by a commissure) is recorded by character 133. Taxa lacking a postorbital process are coded as inapplicable (‘-’) for 133.

Transverse otic process: a transverse wall or process of the otic region that is associated with or supports the hyomandibular articulation. It may be pierced or notched by the jugular canal or imperforate. This structure has generally been referred to as the anterior postorbital process in ‘placoderms’ (e.g. Young 1980: fig. 24). The lateral otic process of some chondrichthyans satisfies these criteria (Extended Data Figure 7), and is coded as a transverse otic process in our analysis. The absence of a prominent otic process in early chondrichthyans like *Pucapampella* and *Doliodus* suggests that the large processes in later taxa like *Tamiodontis* and *Xenacanthus* might be neomorphic (Extended Data Figure 7j; cf. optimizations shown in Supplementary Information 1).

The presence or absence of a transverse otic process is recorded by character 125. Characters 126 and 164 accommodate further variation in the structure of such processes: the presence or absence of a canal for the jugular vein, and position relative to the skeletal labyrinth.

Vagal process(es): lateral extension (or extensions) of the posterior otic region adjacent to foramina for the vagus (X) nerve and associated with facets for the gill skeleton. Brazeau and Friedman (2014) have argued that vagal processes are modified from the branchial ridges of jawless vertebrates. The vagal processes define the anterior margin of an embayment interpreted by Young (1980) as the cucullaris fossa. Our definition is admittedly broad, and we do not presently propose more specific terminology for subcategories of vagal processes (e.g., supravagal and posterior postorbital processes as applied by Young 1980 and others), some of which appear in conjunction. The geometry and size of vagal processes vary considerably among ‘placoderms’, suggesting that more refined classifications of these structures might yield important systematic information. For example, there are two separate vagal processes (according to our criteria for identification) in *Macropetalichthys* and *Kujdanowiaspis* (Extended Data Fig. 7a, c), but only a single process in *Buchanosteus* and *Entelognathus* (Extended Data Fig. 7b, d). Based on our own examination of silicone peels of the rhenanid *Jagorina*, we regard the posterolateral extensions of the braincase in this genus as craniospinal, rather than vagal (Young 1980), processes.

The condition of vagal processes is recorded by character 166.

Craniospinal process: large process extending from the posterolateral corner of the braincase, bearing a distinct craniospinal ridge, and defining the posterior margin of the embayment identified by Young (1980) as the cucullaris fossa. In many ‘placoderms’, this endoskeletal process is intimately associated with the dermal craniothoracic joint (e.g. *Buchanosteus*; Young 1979: fig. 2). A more modest posterolateral extension of the occipital arch, immediately posterior to the metotic fissure, is present in some early actinopterygians (e.g. *Mimipiscis*; Gardiner 1984: fig. 2, ‘crsp’) and has also been termed a craniospinal process (first by Nielsen 1942). A low prominence is present in a comparable location in *Acanthodes* (Miles 1973: pl. 5A, ‘pao.p’; Davis et al. 2012: supp. fig. 9, ‘Pao.p’), but is not nearly as well-developed as the actinopterygian or ‘placoderm’ craniospinal processes, being hardly noticeable in revised reconstructions (Davis et al. 2012 supp. fig. 15). Miles (1977: 55) drew parallels between transverse occipital processes in lungfishes and actinopterygian craniospinal processes, but remained

circumspect concerning their possible homology. Gardiner (1984: 190) regarded the dipnoan and actinopterygian processes as non-homologous.

Despite similarities in orientation and position, the relationship between the craniospinal processes of 'placoderms' and actinopterygians is obscure. What is clear is that the craniospinal processes of actinopterygians are proportionally smaller than, and in some ways structurally distinct from, the processes of the same name in 'placoderms'. However, we are not confident that their homology can be rejected *a priori*. We therefore consider these processes primary homologues, with this hypothesis subject to testing through congruence. This mirrors the strategy applied above for lateral otic/transverse otic processes. Based on mapped character distributions, our analysis rejects homology between the craniospinal processes of actinopterygians and 'placoderms' (Extended Data Figure 7m; cf. optimizations shown in Supplementary Information 1).

The presence or absence of craniospinal processes is recorded by character 167.

Part B. Phylogenetic Analyses

1) Character List

This character list is derived principally from that presented by Davis et al. (2012), itself a modified descendant of Brazeau (2009). The source of additional characters not appearing Davis et al. (2012) are listed in character descriptions. Multistate characters that could be ordered along a morphocline are indicated with an asterisk (*).

Histology

1. [DFC12: 1] Tessellate prismatic calcified cartilage:

Based on our examination of material of *Howqualepis*, we are convinced that the hard tissue surrounding the braincase and other endoskeletal structures in this genus is not prismatic calcified cartilage. We therefore revise the code for this genus to '0'.

0. absent

1. present

2. Prismatic calcified cartilage:

Maisey (2001: character 17), Pradel et al. (2011: character 0).

0. single layered

1. multi-layered

3. [DFC12: 2] Perichondral bone:

Presence of perichondral bone in *Yunnanolepis* is reported by Zhu (1996).

0. present

1. absent

4. [DFC12: 3] Extensive endochondral ossification:

Dicksonosteus and *Macropetalichthys* are scored '0'. Even while some internal ossification has been reported in these taxa (Stensiö 1925; Goujet 1984), it hardly qualifies as being extensive, and the interpretation as endochondral bone is dubious.

0. absent

1. present

5. Enamel(oid) present on dermal bones and scales:

This character, along with the following three, represents an atomization of compound characters relating to suite of features characterizing ganoine and cosmine (e.g. Davis et al. 2012: character 6; Zhu et al. 2013: character 6). A similar approach to atomizing these traits was adopted by Friedman (2007: characters 131, 138 and 195) and Friedman & Brazeau (characters 36 and 37). An enameloid-like capping tissue is reported in thyeostidians by Janvier (1996), so we have coded Osteostraci as polymorphic for this tissue.

0. absent

1. present

6. Enamel:

See notes above for character 5.

- 0. single-layered
- 1. multi-layered

7. Enamel layers:

See notes above for character 5.

- 0. applied directly to one another (ganoine)
- 1. separated by layers of dentine

8. Extensive pore canal network:

See notes above for character 5. Extensive pore canal networks represent a key component of the complex tissue type known as cosmine, but networks of vascular canals that open to the surface of bones and scales by pores are widely distributed among early vertebrates. Best known in sarcopterygians, pore-canal networks are also found in a range of taxa including probable stem osteichthyans (e.g. *Ligulalepis sensu stricto*; Schultze 1968: figs 1-4), acanthodians (e.g. *Poracanthodes*; Valiukevicius 1992: figs 4, 9), and osteostracans (e.g. *Tremataspis*, Denison 1947: fig. 1). Sarcopterygian pore-canal networks are distinguished from these other examples in the density of pore canals, and the flask-like shape of these structures.

- 0. absent
- 1. present

9. [DFC10: 4] Dentinous tissue:

Modified based on Giles et al. (2013). *Onychoselache* and *Tamiobatis* are re-scored '?' based on the absence of figured material documenting this condition. Gross (1947) describes dentine tubules seen in sections through the scales of *Mesacanthus* and *Ischnacanthus*.

- 0. absent
- 1. present

10. [DFC10: 5] Dentine kind:

Lupopsyrus scored '0' based on Hanke & Davis (2012). *Incisoscutum* scored '1' based on Johanson & Smith (2005). Semidentine is reported in *Romundina* (Giles et al. 2013). The precise type of dentine in *Yunnanolepis* is difficult to determine (Giles et al. 2013). Because their dentine is described by Gross (1947) as tubular canals reminiscent of those in similar acanthodians, the dentine type in *Ischnacanthus* and *Mesacanthus* is here scored as orthodentine.

- 0. mesodentine
- 1. semidentine
- 2. orthodentine

11. Bone cell lacunae in body scale bases:

Burrow & Turner (2010: character 61). Hanke & Davis (2008) express uncertainty about bone cell lacunae in the scale bases of *Gladiobranchus*. However, Newman et al. (2012), working on the basis of better-preserved material of *Uraniacanthus* (to which *Gladiobranchus* is synonymous) show convincingly that these lacunae are lacking. *Climatius* is scored '?' in spite of Ørvig's (1967) report of acellular bases. Ørvig figured flat-based scales from the

head. This character strictly concerns body scales, which may have been different. *Cheirolepis* is scored '1' based on Ørvig (1967). However, this is remarkably poorly documented in any accessioned specimens. *Acanthodes* is scored '1' based on Gross (1947) and Valiukevicius (1995). *Dialipina* is scored from Schultze (1968). *Psarolepis* is coded '0' based on Qu et al. (2013). The presence or absence of bone cells in the scale bases of *Brindabellaspis* uncertain based on Burrow & Turner (1999).

- 0. present
- 1. absent

12. Main dentinous tissue forming fin spine:

Burrow & Turner (2010: character 60).

- 0. osteodentine
- 1. orthodentine

Squamation

13. [DFC12: 7] Longitudinal scale alignment in fin webs:

The character formulation of Davis et al. (2012) did not distinguish between ordered arrangements of fin scales and lepidotrichia. Acanthodians and *Dialipina* (uncatalogued specimen, Museum für Naturkunde, Berlin) exhibit fin web scales that are not markedly distinguished from the body scales. Fin web scales of *Dialipina* even include a distinct peg-and-socket articulation. This character thus refers to the alignment only, but not to the specialized rectangle-shaped scales in osteichthyans. *Poracanthodes* is changed to '?' because fin webs do not appear to be preserved in articulated specimens (Valiukevicius 1992). *Brachyacanthus* and *Parexus* scored '1' (pers. obs. SG, NHMUK P.130, P.38593 for *Parexus*, and NHMUK P.6959 and P.9595 *Brachyacanthus*). *Brochoadmones* is scored '0' based on observations on UALVP 41495. *Campbellodus* scored '?'.

- 0. present
- 1. absent

14. Differentiated lepidotrichia:

Refers to the distinct rectangular shape of the aligned lepidotrichia-like scales.

This character is scored contingently on the state of the previous character.

Dialipina is coded '0' (uncatalogued specimen, Museum für Naturkunde, Berlin).

- 0. absent
- 1. present

15. [DFC12: 8] Body scale growth pattern:

Climatius is scored '1' based on Ørvig (1967) showing multiple apposed cusps on the body scales of this taxon. *Onychodus* is re-scored '1'. The scales of *Gemuendina* appear to have only a single external tubercle, implying that they may have been monodontode. However, this is not corroborated by any histological data and so *Gemuendina* is conservatively scored '?'.

- 0. comprising single odontode unit/generation ("monodontode")
- 1. comprising a complex of multiple odontode generations/units ("polyodontode")

- 16. [DFC12: 9] Body scale growth concentric:**
 0. absent
 1. present
- 17. Generations of odontodes:**
 This character is scored contingently on the presence of polyodontote scales.
 Taxa displaying monodontote scales are coded as inapplicable.
 0. buried
 1. areally growing
 2. resorbed
- 18. [DFC12: 10] Body scales with peg-and-socket articulation:**
Lupopsyrus is scored '0', consistent with the description by Hanke & Davis (2012).
 0. absent
 1. present
- 19. Scale peg:**
 Patterson (1982: character 5), Cloutier & Ahlberg (1996: character 4), Dietze (2000: character 57), Schultze & Cumbaa (2001: character 88), Zhu & Schultze (2001: character 199), Zhu et al. (2001: character 145), Zhu & Yu (2002, character 145), Cloutier & Arratia (2004: character 178), Zhu et al. (2006: character 112), Friedman (2007, character 128), Brazeau (2009: character 139), Zhu et al. (2009: character 139), Zhu et al. (2013: character 143).
 0. broad
 1. narrow
- 20. Anterodorsal process on scale:**
 Patterson (1982: character 4), Lauder & Liem (1983: fig. 6, character 4), Gardiner (1984: character 1), Gardiner & Schaeffer (1989: character A20), Schultze (1992: character 2, in part), Schultze & Cumbaa (2001: character 89), Zhu & Schultze (2001: character 201), Zhu et al. (2001: character 146), Zhu & Yu (2002: character 146), Cloutier & Arratia (2004: character 179), Friedman & Blom (2006: character 33), Zhu et al. (2006: character 113), Friedman (2007: character 129), Zhu et al. (2009: character 140), Zhu et al. 2013 (character 144).
 0. absent
 1. present
- 21. [DFC12: 11] Body scale profile:**
Parexus, *Brochoadmones*, *Kathemacanthus*, and *Promesacanthus* are scored '0'. *Buchanosteus* is scored '?'. *Tamiobatis* is scored '0' based on the description by Williams (1998). *Dicksonosteus* and *Pterichthyodes* are scored '1' consistent with Goujet (1984, plate 14, fig. 1) and Hemmings (1978: fig. 22). *Gemuendina* is scored '0'. *Psarolepis* is scored '0' based on Qu et al. (2013).
 0. distinct crown and base demarcated by a constriction ("neck")
 1. flattened
- 22. Profile of scales with constriction between crown and base:**
 This character is scored contingently on the previous character, and thus refers

to necked scales with a pronounced anvil-shaped profile as seen in acanthodids, diplacanthids, ischnacanthids, and similar taxa, and thus is typified by the profile of the *Gomphonchus*-type morphology.

- 0. neck similar in width to crown
- 1. neck greatly constricted, resulting in anvil-like shape

23. [DFC12: 12] Body scales with bulging base:

- 0. absent
- 1. present

24. [DFC12: 13] Body scales with flattened base:

- 0. present
- 1. absent

25. Basal pore in scales:

Growing basal tissue is absent from some scales belonging to chondrichthyans. Although shown only in the cranial cap scales (Coates & Sequeira 2001b: fig. 12E), a basal pore is seen in *Akmonistion*.

- 0. absent
- 1. present

26. [DFC12: 14] Flank scale alignment:

- 0. vertical rows oblique rows or hexagonal
- 1. rhombic packing
- 2. disorganised

27. Scute-like ridge scales (basal fulcra):

Patterson (1982: character 19), Gardiner (1984: character 12), Maisey (1986: N9), Gardiner & Schaeffer (1989: A19), Friedman & Brazeau (2010: character 25).

- 0. absent
- 1. present

28. [DFC12: 15] Sensory line canal:

- 0. perforates scales
- 1. passes between scales
- 2. C-shaped scales

Dermal bones of the skull

29. Dermal ornamentation:

- 0. smooth
- 1. parallel, vermiform ridges
- 2. concentric ridges
- 3. tuberculate

30. [DFC12: 16] Sensory line network:

Galeaspids are recoded as polymorphic based on Donoghue et al. (2000).

- 0. preserved as open grooves (sulci) in dermal bones

1. sensory lines pass through canals in dermal bones (open as pores)
31. **Sensory canals/grooves:**
 Goujet (1984b: unnumbered character), Brazeau (2009: 17). A character similar to this appeared in Brazeau (2009). Davis et al. (2012) did not include this character, but did not elaborate on the rationale behind this deletion. In its present formulation, this character considers the degree to which grooves or canals for sensory lines are expressed as prominent ridges on the visceral surface of dermal bones. This modification reflects the paucity of section data indicating whether the floor of the groove or canal lies deep to the visceral surface of the body of the containing bone.
 0. contained within the thickness of dermal bones
 1. contained in prominent ridges on visceral surface of bone
 32. **[DFC 17] Jugal portion of infraorbital canal joins supramaxillary canal:**
 0. present
 1. absent
 33. **[DFC 18] Dermal skull roof:**
 0. includes large dermal plates
 1. consists of undifferentiated plates or tesserae
 34. **Anterior pit line of dermal skull roof:**
 0. absent
 1. present
 35. **[DFC 19] Tessera morphology:**
 0. large interlocking polygonal plates
 1. microsquamose, not larger than body squamation
 36. **Cranial spines:**
 This character is composed as a compound because there are no further dependent characters. Mathematically, this should be equivalent to atomizing and using inapplicability.
 0. absent
 1. present, multicuspid
 2. present, monocuspid
 37. **[DFC 20] Extent of dermatocranial cover:**
 0. complete
 1. incomplete (limited to skull roof)
 38. **[DFC 21] Openings for endolymphatic ducts in dermal skull roof:**
 Brazeau (2009) and Davis et al. (2012) have scored ptyctodont taxa as lacking endolymphatic duct openings. However, it is unclear if this is the case. Although a small circular foramen is not present in the skull roofs of ptyctodonts, many ptyctodont taxa are described as possessing a "spiracular opening" in their skull roofs (Long 1997; Trinajstić et al. 2012). Because the spiracle of gnathostomes is situated between the hyoid and mandibular arches, we consider this

interpretation extremely doubtful. The purpose of this opening remains unknown, but its interpretation as an endolymphatic opening cannot be ruled out. However, we adopt a conservative approach and code these taxa as '?'. Stensiö (1969) figures *Jagorina* with a posterior dorsal fontanelle and, presumably, interprets this as an endolymphatic opening behind the skull roof. No openings for the endolymphatic ducts are indicated in the skull roof. Examination of the specimen shows that the endolymphatic ducts are parasagittal to the cranial cavity and follow a course up to the skull roof. Because actual openings are not observed, this character is scored '?' for *Jagorina*.

- 0. present
- 1. absent

39. [DFC 22] Endolymphatic ducts with oblique course through dermal skull bones:

- 0. absent
- 1. present

40. Endolymphatic duct relationship to median skull roof bone (i.e. nuchal plate):

- 0. within median bone
- 1. on bones flanking the median bone (e.g. paranuchals)

41. [DFC 25] Pineal opening perforation in dermal skull roof:

This feature is indicated in a reconstruction of *Romundina* (see Goujet & Young 2004, fig. 2), but this is not shown in any specimen photograph or illustration. It is thus unclear whether this is actually observed, or was merely symbolic, indicating the structure's sub-dermal location.

- 0. present
- 1. absent

42. Dermal plate associated with pineal eminence or foramen:

Among taxa sampled in this analysis, osteostracans, antiarchs, *Brindabellaspis*, and *Romundina* bear pineal plates that contribute to the margin of the orbit, corresponding to state '0'. We consider taxa where the pineal foramen is bounded by rectilinear skull roofing bones but which lack separate pineal ossifications (e.g. *Mimipiscis*) as showing state '1'. Taxa lacking macromeric cranial skeletons are coded as inapplicable for this character.

- 0. contributes to orbital margin
plate(s) excluded from orbital margin by skull roofing bones.
- 1. plate bordered laterally by skull roofing bones

43. [DFC 23] Series of paired median skull roofing bones that meet at the dorsal midline of the skull (rectilinear skull roof pattern):

- 0. absent
- 1. present

44. Broad supraorbital vaults:

Dennis & Miles (1981: character 16). This character is contingent on the presence of a dermal skull roof composed of large plates. In coccosteomorph arthrodires,

the dorsal surfaces of the orbits, comprising the preorbital and postorbital plates, are formed of broad, concave laminae. Similar vaults on the visceral surface of the dermal skull are absent in other placoderms and osteichthyans.

- 0. absent
- 1. present

45. Median commissure between supraorbital sensory lines:

- 0. absent
- 1. present

46. Dermal cranial joint at level of sphenoid-otic junction:

Cloutier & Ahlberg (1996: character 81), Ahlberg & Johanson (1998: character 71), Zhu et al. (2001: character 20), Zhu & Schultze (2001: character 31), Zhu & Yu (2002: character 20), Zhu & Ahlberg (2004: character 71), Daeschler et al. (2006: character 50), Long et al. (2006: character 3), Zhu et al. (2006: character 24), Friedman (2007: character 19), Zhu et al. (2009: character 21), Zhu et al. (2013: character 147).

- 0. absent
- 1. present

47. Otic canal extends through postparietals:

Cloutier & Ahlberg (1996: character 101), Zhu & Schultze (2001: character 47), Zhu & Yu (2001: character 37), Zhu & Yu (2002: character 37), Friedman (2007: character 40).

- 0. absent
- 1. present

48. Number of bones of skull roof lateral to postparietals:

Lund et al. (1995: character 21), Cloutier & Ahlberg (1996: character 37), Ahlberg & Johanson (1998: character 49), Zhu & Ahlberg (2004: character 49), Schultze & Cumbaa (2001: character 74), Zhu & Schultze (2001: character 27), Zhu et al. (2001: character 19), Zhu & Yu (2002: character 19), Cloutier & Arratia (2004: character 75), Daeschler et al. (2006: character 39), Zhu et al. (2006: character 22), Friedman (2007: character 18), Zhu et al. (2009: character 27).

- 0. two
- 1. one

49. Suture between paired skull roofing bones (centrals of placoderms; postparietals of osteichthyans):

Modified from Miles & Dennis (1979: character 6)

- 0. straight
- 1. sinusoidal

50. Medial processes of paranuchal wrapping posterolateral corners of nuchal plate:

- 0. absent
- 1. present
- 2. paranuchals precluded from nuchal by centrals
- 3. no median posterior skull roof bone

- 51. Paired pits on ventral surface of nuchal plate:**
Miles & Dennis (1979: character 10), Dennis & Miles (1981: character 10).
0. absent
1. present
- 52. Sclerotic ring:**
Coded according to Burrow et al. (2011).
0. absent
1. present
- 53. [DFC 24] Consolidated cheek plates:**
This character is contingent on dermatocranial cover of the cheek. Taxa lacking any dermal contribution to the cheek are coded as inapplicable.
0. absent
1. present
- 54. Cheek plate:**
This character is contingent on the presence of a consolidated dermal cheek. This character reflects whether the canal-bearing dermal cheek (preopercular or suborbital equivalent) is composed of one or multiple bones. State '0' is apparent in actinopterygians, *Guiyu*, *Psarolepis* (preopercular), *Entelognathus* and other placoderms.
0. undivided
1. divided (i.e., squamosal and preopercular)
- 55. Subsquamosals in taxa with divided cheek:**
Zhu & Schultze (2001: character 64), Zhu & Yu (2001: character 48), Zhu & Yu (2002: character 48), Friedman (2007: character 43).
0. absent
1. present
- 56. Preopercular shape:**
Zhu et al. (2001: character 54), Zhu & Yu (2001: character 54), Friedman (2007: character 48). This character applies only to the subset of sarcopterygians with subdivided cheek plates. In onychodonts (Andrews et al. 2006), porolepiforms (Jarvik 1972), and coelacanth (Forey 1998), the preopercular assumes a plate-like morphology. By contrast, tetrapodomorphs bear a bar-shaped preopercular bone (Jarvik 1980; Long et al. 1997).
0. rhombic
1. bar-shaped
- 57. Vertical canal associated with preopercular/suborbital canal:**
Friedman (2007: character 152, in part).
0. absent
1. present
- 58. [DFC 26] Enlarged postorbital tessera separate from orbital series:**
0. absent

1. present
- 59. Extent of maxilla along cheek:**
 Friedman (2007: character 151), Zhu et al. (2009: character 81), Zhu et al. (2013: character 182). This character is contingent upon the presence of maxillae and a dermal cheek. The jaw bones of ischnacanthids are not part of the external dermal skeleton of the face and jaw (e.g. Blais et al. 2011), and so we do not equate these bones with maxillae/dentaries.
0. to posterior margin of cheek
 1. cheek bones exclude maxilla from posterior margin of cheek
- 60. Dermal neck joint:**
 Zhu et al. (2013: character 169). The presence of a dermal neck joint is not a probable placoderm synapomorphy per se. Rather, the articulation of the shoulder and skull in mandibulate stem gnathostomes is distinguished from the condition in osteichthyans by being a ginglymoid articulation. The articulation in *Brindabellaspis* is peculiar in that it does not appear to be a dermal linkage but was instead an endochondral one (Young 1980).
0. overlap
 1. ginglymoid
- 61. [DFC 15] Sensory line scales/plates on head:**
 See also Burrow & Turner (2010: character 66).
0. unspecialized
 1. apposed growth
 2. paralleling canal
 3. semicylindrical C-shaped ring scales
- 62. [DFC 27] Bony hyoidean gill-cover series (branchiostegals):**
 We have re-coded *Acanthodes* and *Homalacanthus* as '1', reflecting the classic interpretation of the presence of branchiostegal rays in these taxa. Davis et al. (2012) coded the filamentous rays articulating with the hyoid arches of these acanthodids as '0', hypothesizing that they might represent endoskeletal hyoid rays like those present in modern and fossil chondrichthyans. This conclusion was based on overall morphological similarity; the structures in *Acanthodes* and *Homalacanthus* are thin and filamentous, like chondrichthyan hyoid rays and unlike many (but not all) osteichthyan branchiostegal rays. Here we code taxa bearing other ossifications associated with the hyoid arch (e.g. submandibulars, gulars, suboperculars) as '1' for this character.
0. absent
 1. present
- 63. [DFC 28] Branchiostegal plate series along ventral margin of lower jaw:**
 Davis et al. (2012) score for this character in some taxa is changed from '0' to '?' to reflect the lack of knowledge of this character in any figured specimens, or in any specimens cited by the authors. Scores for *Acanthodes* and *Homalacanthus* are changed from '-' to '1' in accordance with the re-evaluation of the hyoidean gill cover series.
0. absent

1. present
- 64. [DFC 29] Branchiostegal ossifications:**
Score for *Ischnacanthus* changed to 1 based on figures presented in Blais et al. (2011).
0. plate-like
 1. narrow and ribbon-like
 2. filamentous
- 65. [DFC 30] Branchiostegal ossifications:**
0. ornamented
 1. unornamented
- 66. [DFC 31] Imbricated branchiostegal ossifications:**
Davis et al. (2012) changed this character to a different definition from Brazeau (2009). It is here reinstated to the original meaning, reflecting the presence of proximal imbrication. *Mesacanthus* is restored to a score of '1'.
0. absent
 1. present
- 67. Median gular:**
Lund et al. (1995: character 64), Cloutier & Ahlberg (1996: character 66), Forey (1998: character 45), Coates (1999: character 11), Lund (2000: character 49), Schultze & Cumbaa (2001: character 84), Zhu & Schultze (2001: character 109), Zhu et al. (2001: character 85), Zhu & Yu (2002: character 85), Lund & Poplin (2002: character 47), Cloutier & Arratia (2004: character 115), Zhu et al. (2006: character 67), Friedman (2007: character 73), Zhu et al. 2009 (character 102), Zhu et al. (2013: character 196).
0. absent
 1. present
- 68. Lateral gular:**
0. absent
 1. present
- 69. [DFC 33] Opercular (submarginal) ossification:**
0. absent
 1. present
- 70. [DFC 34] Shape of opercular (submarginal) ossification:**
0. broad plate that tapers towards its proximal end
 1. narrow, rod-shaped
- 71. [DFC 36] Size of lateral gular plates:**
0. extending most of length of the lower jaw
 1. restricted to the anterior third of the jaw (no longer than the width of three or four branchiostegals)

Ventral hyoid arch and gill skeleton

72. Gill arches:

Scores for certain placoderms without preserved or mineralized gill arch and braincase skeletons are based on the outline of the braincase on the visceral surface of the skull roofing bones and the position of the postbranchial lamina on the shoulder girdle. In placoderms, there is no room for the gill chamber to be extended behind the skull, and must therefore have been placed in a sub-cranial position.

- 0. largely restricted to region under braincase
- 1. extend far posterior to braincase

73. [DFC 37] Basihyal:

The coding for chondrichthyans has been revised following Pradel et al. (2014).

- 0. present
- 1. absent

74. [DFC 38] Interhyal:

We agree with Davis et al. (2012) that the evidence for an interhyal in *Acanthodes* is weak. We retain their coding of '?' here. On the basis of an articulated hyoid arch of *Ischnacanthus* (NHMUK P.7000), we can confirm the absence of the interhyal in that genus and revise the code to '0'.

- 0. absent
- 1. present

75. Hypohyal:

The coding for chondrichthyans has been revised following Pradel et al. (2014). Gardiner (1984: character 27), Maisey (1986: character K11), Friedman & Brazeau (2010: character 12). The hypohyal is a cartilage that lies at the anterior end of the ceratohyal, and links the ventral half of the hyoid arch with the ventral gill skeleton. This character has been considered an osteichthyan synapomorphy (see Friedman & Brazeau 2010 for a review). Davis et al. (2012: 43, supplementary material) query—but do not test—the status of the hypohyal as an osteichthyan synapomorphy, noting occurrences in the chondrichthyans *Debeerius* (Lund & Grogan 2000: fig. 7) and *Cobelodus* (Zangerl & Case 1976: fig. 13). The putative example in *Debeerius* is peculiar, as it articulates with the anterolateral margin of the median basal element, rather than linking the ceratohyal with this basal cartilage. We consider the condition of the mesial hyoid arch in *Cobelodus* to be unclear.

- 0. absent
- 1. present

76. Endoskeletal urohyal:

Friedman (2007: character 164).

- 0. absent
- 1. present

Dentition and jaw bones

77. [DFC 39] Oral dermal tubercles borne on jaw cartilages or at margins of the

mouth:

The original meaning of this character, as formulated by Brazeau (2009) is clarified by an elaborated formulation. Davis et al. (2012) have changed Brazeau's (2009) coding for *Obtusacanthus* from '1' to '0'. This taxon clearly has oral dermal tubercles, manifest as scales on the outer face of the Meckelian cartilage. We restore a score of '1' for this genus. We also code *Bothriolepis* as '1', based on the presence of the denticulated inferognathals described by Young (1984). The score for *Euthacanthus* is changed to '0', contra Davis et al. (2012), as we have not observed teeth in any specimen.

- 0. absent
- 1. present

78. [DFC 39] Oral dermal tubercles patterned in organised rows (teeth):

Teeth are here defined as tubercles borne on the jaw cartilages exhibiting distinct, non-random cusps in serially organised rows.

- 0. absent
- 1. present

79. Enamel(oid) on teeth:

Modified from Rosen et al. (1981: 26), Lauder & Liem (1983: fig. 1, character 17), Gardiner (1984: character 36), Schultze & Cumbaa (2001: character 104), Zhu & Schultze (2001: character 212), Zhu et al. (2001: character 156), Zhu & Yu (2002: character 156), Zhu et al. (2006: character 123), Friedman (2007: character 139), Zhu et al. (2009: character 153). Previous authors have restricted consideration to the presence of 'true' enamel only, a putative synapomorphy of sarcopterygians. Given the ambiguity in differentiating enamel and enameloid in many fossil vertebrates, we adopt a more general formulation of this character.

- 0. absent
- 1. present

80. Cap of enameloid restricted to upper part of teeth (acrodin):

Modified from Patterson (1982: character 12), Gardiner (1984: character 13), Maisey (1986: character N6), Gardiner & Schaeffer (1989: character B1), Cloutier & Ahlberg (1996: character 7), Taverne (1997: character 7), Coates (1999: character 1), Poplin & Lund (2000: character 21), Schultze & Cumbaa (2001: character 35), Zhu & Schultze (2001: character 210), Zhu et al. (2001: character 154), Zhu & Yu (2002: character 154), Cloutier & Arratia (2004: character 32), Gardiner et al. (2005: character 15), Friedman & Blom (2006: character 25), Zhu et al. (2006: character 120), Friedman (2007: character 137), Zhu et al. (2009: character 151), Friedman & Brazeau (2010: character 140), Zhu et al. (2013: character 140). Acrodin tooth caps are widely cited as character uniting most actinopterygians to the exclusion of *Cheirolepis* (Patterson 1982; Gardiner 1984). The presence or absence of acrodin is not well documented for most early actinopterygians, but is clearly present in both *Mimipiscis* and *Moythomasia* (Gardiner 1984).

- 0. absent
- 1. present

81. [DFC 40] Tooth whorls:

We have restored a code of '1' for *Debeerius*, which bears teeth in families corresponding to the definition of whorls applied by Brazeau (2009). The parasymphysial tooth families of this genus align with a more restrictive view of whorls in having joined bases (Grogan & Lund 2000: 226).

- 0. absent
- 1. present

82. [DFC 41] Bases of tooth whorls:

Doliodus is coded here as '0', reflecting the fact that the teeth described by Turner (2004) represent multiple tooth bases united by thin sheets of bone. It seems probable that seemingly 'isolated' teeth of this genus represent broken whorls (Maisey et al. in press).

- 0. single, continuous plate
- 1. some or all whorls consist of separate tooth units

83. [DFC42] Distribution of tooth whorls:

Dialipina (Schultze and Cumbaa 2001), *Eusthenopteron* (Jarvik 1980), *Euthacanthus*, *Gogonasus* (Long et al. 1997), *Mimipiscis* (Gardiner 1984), *Rhamphodopsis* (Miles 1967), and *Tetanopsyrus* (Gagnier et al. 1999) lack tooth whorls, and so are recoded as inapplicable for this character.

- 0. entire length of tooth row
- 1. restricted to symphysial region

84. Distribution of tooth whorls:

- 0. upper and lower jaws
- 1. lower jaws only
- 2. upper jaws only

85. [DFC 43] Teeth ankylosed to dermal bones:

Davis et al. (2012) revised the coding provided by Brazeau (2009) for this character to '1' for *Dicksonosteus*. By the same token, we revise the coding of *Buchanosteus* from '0' to '1' based on the account and figures provided by Young et al. (2001).

- 0. absent
- 1. present

86. Plicidentine:

Cloutier & Ahlberg (1996: character 14), Ahlberg & Johanson (1998: character 14), Schultze & Cumbaa (2001: characters 102-103), Zhu & Schultze (2001: characters 213-215), Zhu et al. (2001: character 157), Zhu & Yu (2002: character 157), Zhu & Ahlberg (2004: character 14), Daeschler et al. (2006: character 10), Long et al. (2006: character 21), Zhu et al. (2006: characters 124-125), Friedman (2007: character 150), Zhu et al. (2009: character 152), Zhu et al. (2009: character 152), Zhu et al. (2013: character 141).

- 0. absent
- 1. present

87. [DFC44] Dermal jaw plates on biting surface of jaw cartilages:

- 0. absent

1. present
- 88. [DFC 45] Maxillary and dentary marginal bones of mouth:**
Modified from Brazeau (2009) and Davis et al. (2012) to omit reference to teeth.
0. absent
 1. present
- 89. Premaxilla:**
Friedman (2007: character 150).
0. extends under orbit
 1. restricted anterior to orbit
- 90. Maxilla shape:**
Lund et al. (1995: character 52), Lund (2000: character 31), Poplin & Lund (2000: character 18), Schultze & Cumbaa (2001: character 31), Zhu & Schultze (2001: character 54), Zhu et al. (2001: character 42), Zhu & Yu (2002: character 42), Lund & Poplin (2002: character 30), Cloutier & Arratia (2004: character 18), Zhu et al. (2006: character 43), Friedman (2007: character 39), Zhu et al. (2009: character 79), Zhu et al. (2013: character 180).
0. splint-shaped
 1. cleaver-shaped
- 91. Pair of tooth plates (anterior supragathals or vomers) on ethmoidal plate:**
0. absent
 1. present
- 92. Strong posterior flexion of dentary symphysis:**
Friedman (2007: character 155).
0. absent
 1. present
- 93. Extent of infradentaries:**
0. along much of ventral margin of dentary
 1. restricted to posterior half of dentary
- 94. Coronoid fangs:**
Ahlberg et al. (2000: character 15), Zhu & Schultze (2001: character 90), Zhu et al. (2001: character 69), Zhu & Yu (2002: character 69), Zhu et al. (2006: character 59), Daeschler et al. (2006: character 71), Long et al. (2006: character 18), Friedman (2007: character 57), Zhu et al. (2009: character 94), Zhu et al. (2013: character 202).
0. absent
 1. present
- 95. Position of upper mandibular arch cartilage (and associated cheek plate where present):**
0. entirely suborbital
 1. with a postorbital extension

- 96. Position of mandibular arch articulations:**
Refers to whether the anteriormost mandibular arch articulations are anterior to the nasal capsules, or immediately below or posterior to them.
- 0. terminal
 - 1. subterminal
- 97. Autopalatine and quadrate:**
Miles & Dennis (1979: character 22); Dennis & Miles (1981: character 22).
- 0. comineralized
 - 1. separate mineralizations
- 98. [DFC 46] Large otic process of the palatoquadrate:**
We have revised the codes for *Poracanthodes* and *Pucapampella* to '1' based on Valiukevicius (1992) and Janvier & Maisey (2010), respectively.
- 0. absent
 - 1. present
- 99. [DFC 47] Insertion area for jaw adductor muscles on palatoquadrate:**
We accept the arguments outlined by Davis et al. (2012) for the lateral insertion of the adductor musculature in ptyctodonts.
- 0. ventral or medial
 - 1. lateral
- 100. Palatoquadrate relationship to dermal cheek bones:**
- 0. broad articulation
 - 1. articulation narrow and restricted
- 101. Palatoquadrate fused with neurocranium:**
- 0. absent
 - 1. present
- 102. [DFC 48] Oblique ridge or groove along medial face of palatoquadrate:**
Relative to the codings provided by Davis et al. (2012), here we change scores for taxa without an expanded posterodorsal region of the palatoquadrate (e.g. 'placoderms') to logical inapplicability.
- 0. absent
 - 1. present
- 103. [DFC 49] Fenestration of palatoquadrate at basipterygoid articulation:**
- 0. absent
 - 1. present
- 104. [DFC 50] Perforate or fenestrate anterodorsal (metapterygoid) portion of palatoquadrate:**
- 0. absent
 - 1. present
- 105. [DFC 51] Pronounced dorsal process on Meckelian bone or cartilage:**
Contrary to the formulation proposed by Davis et al. (2012), the pronounced

dorsal process on the lower jaw of 'acanthodians' like *Gladiobranchus* issues from a dermal plate associated with the mandible rather than the Meckel's cartilage. Consequently, we re-code all taxa lacking dermal lower jaw plates as inapplicable for this character. Burrow & Young (2012: fig. 4b) have recently shown that a similar process is present in *Culmacanthus*, but we find evidence for such a feature lacking in *Diplacanthus* (contra Davis et al. 2012). *Tetanopsyrus* has a high dorsal process of the jaw that seems to be part of the Meckel's cartilage rather than a separate dermal plate like that found in *Gladiobranchus* and *Culmacanthus*. However, we conservatively code this taxon as '?'.

- 0. absent
- 1. present

106. Number of coronoids:

Ahlberg & Clack (1998: character 4), Daeschler et al. (2006: character 5), Long et al. (2006: character 11), Friedman (2007: character 158), Zhu et al. (2009: character 93), Zhu et al. (2013: character 201).

- 0. four or more
- 1. three or fewer

107. [DFC 52] Preglenoid process:

Onychodus and *Poracanthodes* are re-coded as '0'. This structure is not figured in the reconstruction of *Pucapampella* by Janvier & Maisey (2010: fig. 8), but a specimen photograph suggests there is a modest process. A conservative scoring of '?' is nevertheless retained.

- 0. absent
- 1. present

108. [DFC 53] Jaw articulation located on rearmost extremity of mandible:

Previously coded as of uncertain condition, *Tetanopsyrus*, *Pucapampella*, *Poracanthodes*, and *Ptomacanthus* are scored as '0'.

- 0. absent
- 1. present

Neurocranium and associated dermal ossifications

109. [DFC 54] Precerebral fontanelle:

- 0. absent
- 1. present

110. [DFC 55] Median dermal bone of palate (parasphenoid):

Parasphenoids are not preserved for '*Ligulepis*' (Basden and Young 2001), *Pucapampella* (Maisey 2001), or *Janusiscus*. We follow the convention, applied to other taxa in our analysis known from well-preserved neurocrania lacking parasphenoids, and code these genera as '0'.

- 0. absent
- 1. present

111. Parasphenoid:

Friedman (2007: character 168), Zhu et al. (2009: character 68).

- 0. lozenge-shaped
 - 1. splint-shaped
- 112. [Z13 241] Multifid anterior margin of parasphenoid denticle plate:**
Friedman (2007: character 167), Zhu et al. (2009: character 69), Zhu et al. (2013: character 241).
- 0. absent
 - 1. present
- 113. Enlarged ascending processes of parasphenoid:**
Modified from Patterson (1982: character 9), Dietze (2000: character 54); Schultze & Cumbaa (2001: character 52), Zhu and Schultze (2001: character 125), Cloutier & Arratia (2004: character 123), Friedman & Blom (2006: character 28), Zhu et al. (2006: character 70), Zhu et al. (2009: character 67), Zhu et al. (2013: character 239).
- 0. absent
 - 1. present
- 114. Buccohypophysial canal in parasphenoid:**
- 0. single
 - 1. paired
- 115. [DFC 56] Nasal opening(s):**
The score for *Austroptyctodus* is changed to '?'. The opening is a dermal structure, and there is no dermal preservation around the nostrils of *Austroptyctodus* (Long 1997).
- 0. dorsal, placed between orbits
 - 1. ventral and anterior to orbit
- 116. Posterior nostril:**
Cloutier & Ahlberg (1996: character 46), Schultze & Cumbaa (2001: character 23); Zhu & Schultze (2001: character 40), Zhu et al. (2001: character 27), Zhu & Yu (2002: character 27), Friedman & Blom (2006: character 6), Zhu et al. (2006: character 31), Friedman (2007: character 25), Zhu et al. (2009: character 8), Zhu et al. (2013: character 152).
- 0. separated from orbital fenestra
 - 1. confluent with orbital fenestra
- 117. [DFC 57] Olfactory tracts:**
Reflecting incomplete neurocranial data, the code for *Austroptyctodus* is changed to '?'. Zhu et al. (2013) report short olfactory tracts in *Psarolepis* (IVPP V11490.2), and we revise the coding of this genus to '0'. We also accept their revision of the state in *Onychodus* to '?'.
0. short, with olfactory capsules situated close to telencephalon cavity
1. elongate and tubular (much longer than wide)
- 118. [DFC 58] Prominent pre-orbital rostral expansion of the neurocranium:**
Chondrenchelys and *Debeerius* changed to '0', contra Davis et al. (2012). There is a prominent pre-orbital expansion in these taxa.

- 0. present
- 1. absent

119. [DFC 59] Pronounced sub-ethmoidal keel:

Here we revise scores presented by Davis et al. (2012) for *Debeerius*, *Chondrenchelys*, and *Tamiobatis* to '?'. There are no satisfactory published ventral views of the neurocranium in *Debeerius* (Grogan & Lund 2000) and *Chondrenchelys* (Moy-Thomas 1935). *Tamiobatis* preserves part of a structure that might be part of a sub-ethmoidal keel, but this is damaged and we adopt a more agnostic stance on the condition in this taxon.

- 0. absent
- 1. present

120. Internasal vacuities:

Zhu & Schultze (2001: character 139), Zhu et al. (2001: character 105), Zhu & Yu (2002: character 105), Friedman (2007: character 91).

- 0. absent
- 1. present

121. Discrete division of the ethmoid and more posterior braincase at the level of the optic tract canal:

The intracranial division has been dismissed as a potential placoderm synapomorphy on the basis that it is a primitive vertebrate character (Goujet 2001). It was therefore omitted by Brazeau (2009). However, the character is reinstated here because the belief that it is a primitive feature based on comparisons with taxa such as lamprey and embryos, which have no perichondral lining of the braincase, are not relevant to the question of adult conditions in either ingroup or outgroup taxa. A division as observed in nearly all placoderm taxa for which a braincase has been described is demonstrably and equivalently absent in galeaspids, osteostracans, osteichthyans, chondrichthyans, and *Ptomacanthus*. The condition in *Acanthodes* is unknown.

- 0. absent
- 1. present

122. [DFC 60] Position of myodome for superior oblique eye muscles:

- 0. posterior and dorsal to foramen for nerve II
- 1. anterior and dorsal to foramen

123. [DFC 61] Endoskeletal intracranial joint:

- 0. absent
- 1. present

124. [DFC 62] Spiracular groove on basicranial surface:

Contra Davis et al. (2012), Yu (1998) identifies a "prespiracular groove" in *Psarolepis*. Available figures of *Guiyu* are unclear, and the specimens quite distorted from one individual to another, especially in this region. This renders interpretation very difficult. However, Davis et al. (2012) scored these taxa and the braincase referred to *Ligulalepis* conservatively as '?'. We provisionally retain this scoring, except for *Psarolepis*, where we accept the interpretation provided by

Yu (1998) and code this taxon as '1'.

- 0. absent
- 1. present

125. Transverse otic process :

Schaeffer (1981), Coates & Sequeira (1998). This character refers to the presence of a transverse wall or process of the otic region that supports the hyomandibular articulation. Such a structure is present in many placoderms (the anterior postorbital process of traditional nomenclature), chondrichthyans (the lateral otic process), and osteichthyans (the lateral commissure sensu lato). There is some variability in the structure (pierced by jugular canal versus imperforate) and location (level with the anterior or posterior of the otic capsule) of transverse otic processes among early gnathostomes. We describe these patterns of variability in characters 126 and 164.

- 0. present
- 1. absent

126. Jugular canal:

This character is modified from DFC characters 76 and 93. In part, this character describes patterns of variation among transverse otic processes that bear the hyomandibular facet (see characters 125 and 164). Transverse otic processes that lack a canal for the jugular are characteristic of many chondrichthyans (e.g. *Tamiobatis*, *Orthacanthus*). In cases where taxa lack a jugular canal and have a posteriorly positioned transverse otic process, this structure is typically called a lateral otic process (e.g. Schaeffer 1981: figs. 6, 21; Coates & Sequeira 1998: fig. 6). This character is composed as a compound because there are no further dependent characters. Mathematically, this should be equivalent to atomizing and using inapplicability.

- 0. long (invested in otic region along length of skeletal labyrinth)
- 1. short (restricted to region anterior of skeletal labyrinth)
- 2. absent (jugular vein uninvested in otic region)

127. [DFC 63] Spiracular groove on lateral commissure:

Here we consider the relationship between the spiracular groove and the lateral commissure sensu lato (see Table 2 above). We have revised the coding given by Davis et al. (2012) for *Gogonasmus* to '1', as this taxon shows a similar condition to *Eusthenopteron* (compare Long et al. 1997: fig. 22 and Jarvik 1980: fig. 86). Osteostraci, Galeaspida, *Brindabellaspis*, and *Macropetalichthys* are scored as inapplicable for this character.

- 0. absent
- 1. present

128. [DFC 64] Subpituitary fenestra:

We have revised the score for *Gogonasmus* to '0' following Long et al. (1997).

- 0. absent
- 1. present

129. [DFC 65] Supraorbital shelf broad with convex lateral margin:

Coding for *Doliodus* restored to '1', contra Davis et al. (2012). The broad

supraorbital shelf with a convex lateral margin is clearly present in tomography renderings of *Doliodus* presented by Maisey et al. (2009). It is true that *Akmonistion* and *Cladoselache* exhibit a much more similar, highly pronounced condition, this being related to a much wider postorbital span in these taxa.

- 0. absent
- 1. present

130. [DFC 66] Orbit dorsal or facing dorsolaterally, surrounded laterally by endocranium:

Ptyctodonts are all scored as '?', contra Davis et al. (2012). Given the lack of complete endocranial data, the antorbital position for the hyomandibular articulation, and the presence of a suborbital lamina of the marginal bone of ptyctodonts, there is a distinct possibility that there is a comparable extension of the neurocranial wall as in *Brindabellaspis*, *Macropetalichthys*, and agnathan outgroups. We have therefore coded the condition in ptyctodonts as uncertain. Although rhenanids have dorsally facing orbits they lack any kind of posterior or ventral orbital processes. They are therefore coded as '1'.

- 0. present
- 1. absent

131. Eyestalk attachment area:

Zhu and Schultze (2001: character 147), Zhu et al. (2001: character 109), Zhu & Yu (2002: character 109), Zhu et al. (2006: character 83), Friedman (2007: character 95), Zhu et al. (2009: character 36), Zhu et al. (2013: character 222).

- 0. absent
- 1. present

132. Postorbital process:

Here we define the postorbital process as a dorsally positioned process at the rear margin of the orbit. The postorbital process is known by a variety of names in different groups: suprapterygoid process (sarcopterygians: Jarvik 1980); supraorbital process (placoderms: Stensio 1969; Jarvik 1980); postorbital pila (in part; identified in some early sarcopterygians and *Entelognathus*, where a bridge encloses the jugular vein: Yu 1998; Zhu et al. 2013); lateral commissure (in part; identified in early actinopterygians and *Ligulalepis*; Zhu et al. 2013).

Rudimentary postorbital processes are present in the rhenanid *Jagorina* (Stensio 1969: fig. 90) and the porolepiforms *Porolepis* and *Glyptolepis* (Jarvik 1972: figs 20-21). Taxa in which the orbit is completely enclosed by the neurocranium (e.g. *Macropetalichthys*) or where the palatoquadrate is fused to the neurocranium (e.g. *Helodus*) are coded as uncertain for this character.

- 0. absent
- 1. present

133. Canal for jugular in postorbital process:

- 0. absent
- 1. present

134. Series of perforations for innervation of supraorbital sensory canal in supraorbital shelf:

This character is coded as inapplicable in taxa lacking well-developed supraorbital shelves.

- 0. absent
- 1. present

135. [DFC 67] Extended prehypophysial portion of sphenoid:

- 0. absent
- 1. present

136. [DFC 68] Narrow interorbital septum:

Davis et al. (2012) code this character as '1' in pttyctodonts based on Long's (1997) interpretation, but cite it as tentative. Because this relies on a reconstruction of medio-laterally flattened fossils, these scores are changed to '?'. The interorbital space in *Gogonasus* and *Eusthenopteron* is quite narrow, and this is recoded as '1' for these taxa. *Acanthodes* and *Howqualepis* are scored '?' because the interorbital space can only be inferred.

- 0. absent
- 1. present

137. [DFC 69] The main trunk of facial nerve (N. VII):

The braincase referred to *Ligulalepis* is scored '?' due to variable interpretations of the position and identity of the jugular canal in this taxon (Basden & Young 2001; Friedman & Brazeau 2010; Davis et al. 2012).

- 0. elongate and passes anterolaterally through orbital floor
- 1. stout, divides within otic capsule at the level of the transverse otic wall

138. [DFC 70] Course of hyoid ramus of facial nerve (N. VII) relative to jugular canal:

This character is coded as inapplicable for taxa that lack skeletal enclosure of the jugular vein within the otic capsule, as well as in osteostracans and galeaspids where the hyoid ramus of the facial nerve exits in the orbit (see previous character).

- 0. traverses jugular canal, with separate exit in otic region
- 1. intersects jugular canal, with exit through posterior jugular foramen

139. [DFC 71] Glossopharyngeal nerve (N. IX) exit:

The case for the placement of N. IX in *Acanthodes* by Davis et al. (2012) is problematic. The groove interpreted as the passage of the glossopharyngeal nerve in *Acanthodes* is also present in the braincase referred to *Ligulalepis*. So, either we must reinterpret the course of its glossopharyngeal nerve, or consider that this groove has no significance for the course of the glossopharyngeal nerve. We adopt a conservative approach, and code the condition in *Acanthodes* as '?'. We adopt a conservative approach, and code the condition in *Acanthodes* as '?'.

- 0. foramen situated posteroventral to otic capsule and anterior to metotic fissure
- 1. through metotic fissure

140. [DFC 74] Relationship of cranial endocavity to basisphenoid:

Reformulated from Brazeau (2009) and Davis et al. (2012). Formerly a distinction between tropibasy and platybasy, this character has been revised to

use more descriptive terms and avoid embryological baggage and typology. The condition referring to the precise proportions of this feature (i.e. as septate or broad) are accounted for in character 135. Taxa for which this cannot be directly observed have been recoded to '?'. *Acanthodes* has been scored similarly because this region is not mineralised.

- 0. endocavity occupies full depth of sphenoid
- 1. endocavity dorsally restricted

141. Subcranial ridges:

Subcranial ridges were first described in *Doliodus* by Maisey et al. (2009). These ridges extend along the ventrolateral corner of the basicranium from the level of the hypophysis up to the hyomandibular articulation. These ridges have not previously been recognized in other early gnathostomes prior to our observations in *Janusiscus*. It is apparent from our revised comparative anatomy of early gnathostome braincases that subcranial ridges are present in the braincase referred to *Ligulalepis*, where they are manifest as downturned margins of the ventral surface of the sphenoid (Basden & Young 2001), and *Mimipiscis* (Gardiner 1984: fig. 50), where they greatly reduced in length.

- 0. absent
- 1. present

142. [DFC 75] Ascending basisphenoid pillar pierced by common internal carotid:

There is ambiguity in assessing this character for any taxon for which the endocast has not been described in detail. Scores for *Guiyu*, *Psarolepis*, *Porolepis*, *Tristychius* and *Gogonasus* are changed to '?' as there is no adequate documentation of the endocranial cavity in these taxa.

- 0. absent
- 1. present

143. [DFC 77] Canal for lateral dorsal aorta within basicranial cartilage:

- 0. absent
- 1. present

144. [DFC 78] Entrance of internal carotids:

Zhu et al. (2013) propose revised codes of '0' for *Porolepis*, *Psarolepis*, and *Guiyu*. We accept these changes for *Porolepis* and *Psarolepis*, but retain a code of '?' for *Guiyu* owing to unclear conditions in published figures.

- 0. through separate openings flanking the hypophyseal opening or recess
- 1. through a common opening at the central midline of the basicranium

145. [DFC 79] Canal for efferent pseudobranchial artery within basicranial cartilage:

- 0. absent
- 1. present

146. [DFC 80] Position of basal/basipterygoid articulation:

Doliodus has been scored as polymorphic for this character because it represents a combination of both conditions. The orbital articulation appears to be

coextensive with most of the length of the suborbital ridge (Maisey et al. 2009). The ridge is distinctly wider at the level of the hypophysial opening, which recalls the weak basiptyergoid articulation in the braincase referred to *Ligulalepis* (Basden & Young 2001; MDB pers. obs. 2007).

- 0. same anteroposterior level as hypophysial opening
- 1. anterior to hypophysial opening

147. [DFC: 81] Articulation between neurocranium and palatoquadrate posterodorsal to orbit (suprapterygoid articulation):

We reformulate this character to consider articulations between the palatoquadrate and dorsal regions of the neurocranium, regardless of whether the latter features are generally called 'postorbital processes' or not. This effectively represents a restoration of character 82 of Brazeau (2009). Outside of chondrichthyans and some acanthodians, articulations between the dorsal portion of the palatoquadrate and neurocranium are present in many sarcopterygian osteichthyans. Both *Eusthenopteron* (Jarvik 1980: fig. 86) and *Porolepis* (Jarvik 1972: fig. 20) bear clear facets on the neurocranium for a suprapterygoid articulation, and are recoded as '1'. Conditions of the neurocranium of *Gogonassus* are unclear, but the processus ascendens of the palatoquadrate in this genus appears to bear a clear articular facet (Long 1997: 30). We therefore recode this taxon as '1'.

- 0. absent
- 1. present

148. [DFC 82] Labyrinth cavity:

Davis et al. (2012) code *Austroptyctodus* with state '1', citing Long (1997), Miles & Young (1977), and personal communication from K. Trinajstić (citing no date and no specimen numbers) in support of the statement "the basicranial ossifications include no evidence of the base of a medial capsular wall". This is a highly equivocal statement. The basicranial ossifications show no compelling evidence of the skeletal labyrinth or even the cranial cavity. They are highly incomplete in the extent of their ossification. *Austroptyctodus*, and other ptyctodonts, must be scored indicating missing data.

- 0. separated from the main neurocranial cavity by a cartilaginous or ossified capsular wall
- 1. skeletal capsular wall absent

149. [DFC 83] Basiptyergoid process (basal articulation) with vertically oriented component:

- 0. absent
- 1. present

150. [DFC 84] Pituitary vein canal:

- 0. dorsal to level of basiptyergoid process
- 1. flanked posteriorly by basiptyergoid process

151. [DFC 85] External (horizontal) semicircular canal:

- 0. absent
- 1. present

152. [DFC 86] Sinus superior:

- 0. absent or indistinguishable from union of anterior and posterior canals with saccular chamber
- 1. present

153. [DFC 87] External (horizontal) semicircular canal:

- 0. joins the vestibular region dorsal to posterior ampulla
- 1. joins level with posterior ampulla

154. Horizontal semicircular canal in dorsal view:

This character captures the variable relationship between the course of the jugular vein and the horizontal semicircular canal. In placoderms, the jugular canal extends lateral to the horizontal canal in dorsal view, whereas most crown gnathostomes show a contrasting condition where the vein is overlapped by the canal. Galeaspid and osteostracans lack a horizontal canal, and are coded as inapplicable for this character.

- 0. medial to path of jugular vein
- 1. dorsal to jugular vein

155. Lateral cranial canal:

Gardiner (1984: character 19), Gardiner & Schaeffer (1989: character 5, C1), Coates (1999: character 32), Cloutier & Arratia (2004: character 1), Gardiner et al. (2005: character 5), Zhu et al. (2006: character 91), Zhu et al. (2009: character 55), Zhu et al. (2013: character 233).

- 0. absent
- 1. present

156. [DFC 88] Trigemino-facial recess:

- 0. absent
- 1. present

157. [DFC 89] Posterior dorsal fontanelle:

Stensiö (1969: fig. 25) figures a posterior dorsal fontanelle in *Jagorina*, but examination of MB.f.510.5-6 shows that this part of the braincase was covered by skull roofing bones. It is therefore not possible to confirm Stensiö's reconstruction, and we consider it here to be inferential. However, we do note that he figured a similar opening for *Asterosteus* (Stensiö 1969: figs. 30C, 92-93).

- 0. absent
- 1. present

158. [DFC 90] Shape of posterior dorsal fontanelle:

- 0. approximately as long as broad
- 1. much longer than wide, slot-shaped

159. Synotic tectum:

Coates & Sequeira (1998: character 9).

- 0. absent
- 1. present

160. [DFC 91] Dorsal ridge:

Like other dorsal ridges present in fish skulls, the dorsal ridge of the endocranium found in some chondrichthyans and acanthodians likely marks the division between the insertion of paired epaxial musculature. Because this arrangement is contingent upon the presence of such insertions on the dorsal surface of the neurocranium, we have coded this character as inapplicable for taxa with dermal skull roofs.

- 0. absent
- 1. present

161. Shape of median dorsal ridge anterior to endolymphatic fossa:

Modified from Coates & Sequeira (1999: character 11), Coates & Sequeira (2001a: character 75), Coates & Sequeira (2001b: character 9) and Maisey (2001: character 9).

- 0. developed as a squared-off ridge or otherwise ungrooved
- 1. bears a midline groove

162. [DFC 92] Endolymphatic ducts in neurocranium:

Zhu et al. (2013) revised the coding for *Cowralepis* to '0', citing the arrangement of impressions on the visceral surface of the dermal skull roof in this taxon. However, no endocranium is preserved in *Cowralepis*, and the present character refers explicitly to the course of these ducts within the neurocranium. We therefore restore a code of '?'.
0. posteriodorsally angled tubes
1. tubes oriented vertically through median endolymphatic fossa

- 0. posteriodorsally angled tubes
- 1. tubes oriented vertically through median endolymphatic fossa

163. [DFC 95] Position of hyomandibula articulation on neurocranium:

- 0. below or anterior to orbit, on ventrolateral angle of braincase
- 1. on otic capsule, posterior to orbit

164. [DFC 93, in part] Position of hyomandibula articulation relative to structure of skeletal labyrinth:

This character can be coded for taxa that either lack or bear a transverse otic process. We consider this a more precise statement of the relative placement of the hyomandibular articulation in most chondrichthyans by comparison with other gnathostomes. This character also captures whether the transverse otic process is level with the anterior part of the otic region, as in placoderms and osteichthyans, or is more posteriorly placed, as in chondrichthyans.

- 0. anterior or lateral to skeletal labyrinth
- 1. at level of posterior semicircular canal

165. [Z13: 227] Hyoid arch articulation on braincase:

Cloutier & Ahlberg (1998: character 88), Zhu & Schultze (2001: character 128), Schultze & Cumbaa (2001: character 53), Zhu et al. (2001: character 96), Zhu & Yu (2002: character 96), Zhu et al. (2006: character 73), Friedman (2007: character 84), Zhu et al. (2009: character 44), Zhu et al. (2013: character 228).

- 0. single
- 1. double

166. Branchial ridges:

Here we define the vagal process as a lateral extension (or extensions) of the posterior otic region that are associated with foramina for branches of the vagus (X) nerve and bear facets for the branchial arches. They can also be pierced by the jugular canal. Vagal processes are well developed in placoderms (e.g. *Dicksonosteus*; Goujet 1984: fig 6). A complete account of vagal processes is provided above in section 3 ('Lateral Processes of Early Gnathostome Neurocrania').

- 0. present
- 1. reduced to vagal process
- 2. absent (articulation made with bare cranial wall)

167. Craniospinal process:

The craniospinal process forms the posterolateral corner of the braincase and is often involved with or supports the cranio-thoracic joint. A complete account of the craniospinal process is provided above in section 3 ('Lateral Processes of Early Gnathostome Neurocrania').

- 0. absent
- 1. present

168. [DFC 96] Ventral cranial fissure:

- 0. absent
- 1. present

169. Basicranial fenestra:

Ahlberg & Johanson (1998: character 76), Zhu et al. (2001: character 114), Zhu and Yu (2002: character 114), Zhu & Ahlberg (2004: character 76), Daeschler et al. (2006: character 52), Long et al. (2006: character 34), Friedman (2007: character 100), Zhu et al. (2009: character 52), Zhu et al. (2013: character 231).

- 0. absent
- 1. present

170. [DFC 97] Metotic (otic-occipital) fissure:

- 0. absent
- 1. present

171. [DFC 98] Vestibular fontanelle:

- 0. absent
- 1. present

172. [DFC 99] Occipital arch wedged in between otic capsules:

- 0. absent
- 1. present

173. [DFC 100] Spino-occipital nerve foramina:

- 0. two or more, aligned horizontally
- 1. one or two, dorsoventrally offset

174. [DFC 101] Ventral notch between parachordals:

This is changed to '?' for galeaspids as the notochordal space is unindicated by Gai et al. (2011). *Cowralepis* is changed to '0' as the parachordal plates are unfused, even though they are closely adpressed.

- 0. present or entirely unfused
- 1. absent

175. [DFC 102] Parachordal shape:

Modified from Brazeau (2009). Previous formulation was: "Parachordal shape: broad, flat (0); keeled with sloping lateral margins (1)." The parachordals might not necessarily slope, but they may be considerably narrower than the otic capsules; the base of the parachordals might be considerably more ventral than the otic capsules.

- 0. forming a broad, flat surface as wide as the otic capsules
- 1. mediolaterally constricted relative to the otic capsules

176. Stalk-shaped parachordal/occipital region:

In petalichthyids such as *Macropetalichthys*, the occiput is flanked by large cucullaris fossae, resulting in a very elongate and narrow occipital region (Stensiö 1969; Young 1978). Although the endocranium of *Lunaspis* is not known in any external preparations, the stalked occiput is clearly visible in a radiograph prepared by W. Stürmer (SMF WS 10825) of an isolated skull from the Hunsrück Slate.

- 0. absent
- 1. present

177. Paired occipital facets:

- 0. absent
- 1. present

178. Size of aperture to notochordal canal:

- 0. much smaller than foramen magnum
- 1. as large, or larger, than foramen magnum

179. Canal for median dorsal aorta within basicranium:

Coates & Sequeira (1998: character 3), Coates & Sequeira (2001a: character 68), Coates & Sequeira (2001b: character 68), Friedman (2007: character 183), Zhu et al. (2009: character 51), Friedman & Brazeau (2010: character 38), Zhu et al. (2013: character 234).

- 0. absent
- 1. present

180. [DFC 103] Hypotic lamina (and dorsally directed glossopharyngeal canal):

Presence of a hypotic lamina is contingent on the retention of an otoccipital fissure between the parachordals and otic capsule. We therefore code all taxa lacking a persistent fissure as inapplicable. Although Davis et al. (2012) argue for the presence of a hypotic lamina in *Chondrenchelys*, its condition cannot be assessed. We therefore recode this taxon as '?'.

- 0. absent

1. present

Paired fins and girdles

181. [DFC 104] Macromeric dermal shoulder girdle:

0. present
1. absent

182. [DFC 105] Dermal shoulder girdle composition:

0. ventral and dorsal (scapular) components
1. ventral components only

183. [CA96: 115] Shape of dorsal blade of dermal shoulder girdle (either cleithrum or anterolateral plate):

Cloutier & Ahlberg (1996: character 115), Schultze & Cumbaa (2001: character 94), Zhu & Schultze (2001: character 164), Zhu et al. (2001: character 122), Zhu & Yu (2002: character 122), Cloutier & Arratia (2004: character 148), Zhu et al. (2006: character 96), Friedman (2007: character 107), Zhu et al. (2009: character 124).

0. spatulate
1. pointed

184. [DFC 106] Dermal shoulder girdle forming a complete ring around the trunk:

0. present
1. absent

185. [DFC 107] Pectoral fenestra completely encircled by dermal shoulder armour:

0. present
1. absent

186. [DFC 108] Median dorsal plate:

0. absent
1. present

187. Posterior dorsolateral (PDL) plate or equivalent:

0. absent
1. present

188. [DFC 109] Pronounced internal crista (keel) on median dorsal surface of shoulder girdle:

0. absent
1. present

189. [DFC 109] Crista internalis of dermal shoulder girdle:

0. absent
1. present

- 190. Scapular infundibulum:**
This character refers to the dermal opening for the scapulocoracoid. In antiarchs, the scapula is situated within an infundibulum, rather than a fenestration.
0. absent
1. present
- 191. [DFC 110] Scapular process of shoulder endoskeleton:**
0. absent
1. present
- 192. [DFC 111] Ventral margin of separate scapular ossification:**
0. horizontal
1. deeply angled
- 193. [DFC 112] Cross sectional shape of scapular process:**
0. flattened or strongly ovate
1. subcircular
- 194. [DFC 113] Flange on trailing edge of scapulocoracoid:**
0. absent
1. present
- 195. [DFC 114] Scapular process with posterodorsal angle:**
Culmacanthus is scored as '?' because scapulocoracoids associated with a specimen of this taxon shows an inflection resembling a posterodorsal angle (Burrow & Young 2012: fig. 2 f, g). However, this is not seen in other specimens. *Onychoselache* and *Hamiltonichthys* are re-coded '1' based on photographs and specimen illustrations (Maisey 1989: fig. 14; Coates & Gess 2007: fig. 5).
0. absent
1. present
- 196. [DFC 115] Endoskeletal postbranchial lamina on scapular process:**
We have revised the coding for *Austroptyctodus* to '0' (Long 1997).
0. present
1. absent
- 197. [DFC 116] Mineralisation of internal surface of scapular blade:**
0. mineralised all around
1. unmineralised on internal face forming a hemicylindrical cross-section
- 198. [DFC 117] Coracoid process:**
0. absent
1. present
- 199. [DFC 118] Procoracoid mineralisation:**
0. absent
1. present
- 200. [DFC 119] Fin base articulation on scapulocoracoid:**

Guiyu and *Psarolepis* re-scored as '1'. *Acanthodes* scored '1'. Conditions in ptyctodonts are uncertain, but there is clearly more than one position for fin basals, often broadly separated (Miles & Young 1977; Trinajstić et al. 2012). *Debeerius* is scored '1' as the articulation is indicated as being quite broad (Grogan & Lund 2000).

- 0. deeper than wide (stenobasal)
- 1. wider than deep (eurybasal)

201. Pectoral fin articulation:

Zhu & Schultze (2001: character 175), Zhu et al. (2001: character 129), Zhu & Yu (2002: character 129), Zhu et al. (2006: character 104), Friedman (2007: character 113), Zhu et al. (2009: character 130), Zhu et al. (2013: character 130).

- 0. monobasal
- 1. polybasal

202. Number of basals in polybasal pectoral fins:

- 0. three or more
- 1. two

203. Branching radials in paired fins:

Complex patterns of branching radials are ubiquitous in the paired fins of crown gnathostomes. This branching is typically associated with the posterior margin of rear fins generally and the metapterygium specifically. By contrast, the basal support of osteostracan paired appendages consist of unbranched plates, while those of many placoderms appear to be constructed of parallel rows of simplified, unbranched radials.

- 0. absent
- 1. present

204. Number of mesomeres in metapterygial axis:

Cloutier & Ahlberg (1996: character 123), Zhu & Schultze (2001: character 180), Zhu & Yu (2001: character 132), Zhu & Yu (2002: character 132), Friedman (2007: character 115).

- 0. five or fewer
- 1. seven or more

205. Biserial pectoral fin endoskeleton:

- 0. absent
- 1. present

206. [DFC 120] Perforate propterygium:

- 0. absent
- 1. present

207. Filamentous extension of pectoral fin from axillary region:

- 0. absent
- 1. present

208. [DFC 121] Pelvic fins:

- 0. absent
- 1. present

209. [DFC 122] Pelvic claspers:

Cladoselache is coded as '1' based on the clasper-like appendage figured by Hussakof & Bryant (1916) (cf. Maisey 2008). Long et al. (2009) argue for the presence of claspers in *Cowralepis*, so we revise the code of this taxon to '1'.

- 0. absent
- 1. present

210. [DFC 123] Dermal pelvic clasper ossifications:

The presence of dermal pelvic clasper ossifications is contingent on the presence of claspers. We therefore code all taxa lacking claspers as inapplicable for the present character. All taxa for which the presence of claspers cannot be determined are coded as '?'.
0. absent
1. present

- 0. absent
- 1. present

211. [DFC 124] Pectoral fins covered in macromeric dermal armour:

- 0. absent
- 1. present

212. [DFC 125] Pectoral fin base has large, hemispherical dermal component:

- 0. absent
- 1. present

Axial skeleton including median fins and their supports

213. [DFC 126] Dorsal fin spines:

A spine-like midline ossification is present at the anterior margin of the dorsal fin of *Pterichthyodes* (Hemmings 1978), so we code this taxon as '1'.

- 0. absent
- 1. present

214. [DFC 127] Anal fin spine:

- 0. absent
- 1. present

215. [DFC 128] Paired fin spines:

- 0. absent
- 1. present

216. [DFC 129] Median fin spine insertion:

- 0. shallow, not greatly deeper than dermal bones/scales
- 1. deep

217. [DFC 130] Intermediate fin spines:

- 0. absent
- 1. present

218. Fin spine cross-section:

Early gnathostome fin spines have at least two distinctive profiles in cross-section. Generally, the profile is gently curving or parabolic. Taxa such as acanthodids and ischnacanthids exhibit a condition in which the cross-section is more rectangular, and the sides of the spine are flatter and closer to parallel (Denison 1979; Gagnier & Wilson 1996).

- 0. Round or horseshoe shaped
- 1. Flat-sided, with rectangular profile

219. Intermediate spines when present:

- 0. one pair
- 1. multiple pairs

220. [DFC 131] Prepectoral fin spines:

- 0. absent
- 1. present

221. [DFC 132] Fin spines with ridges:

- 0. absent
- 1. present

222. [DFC 133] Fin spines with nodes:

- 0. absent
- 1. present

223. [DFC 134] Fin spines with rows of large retrorse denticles:

- 0. absent
- 1. present

224. Expanded spine rib on leading edge of spine:

This character is common to acanthodids and their proximal relations. It is variably present in *Kathemacanthus*.

- 0. absent
- 1. present

225. Spine ridges:

- 0. converging at the distal apex of the spine
- 1. converging on leading edge of spine

226. [DFC 135] Synarcual:

- 0. absent
- 1. present

227. Series of thoracic supraneurals:

Cloutier & Ahlberg (1996: character 137), Ahlberg & Johanson (1998: character 99), Zhu & Ahlberg (2004: character 99), Zhu & Yu (2001: character 142), Zhu & Yu (2001: character 142), Friedman (2007: character 125).

- 0. absent

1. present

228. [DFC 136] Number of dorsal fins, if present:

0. one
1. two

229. Posterior dorsal fin shape:

This is admittedly a compound character. This owes to the problems of rendering ratio-scale continuous characters as a discrete character. Our conceptualisation of this character is intended to capture the distinctively broad or ribbon-shaped second dorsal fins that are differentiated from any of the other median fins, and the generalized triangular shape of many gnathostomes and their relatives. In taxa possessing only a single dorsal fin, we have scored taxa where we think the observed fin is equivalent to a posterior dorsal fin. This is based on the position of the posterior dorsal fin behind or at the level of the posterior limit of the posterior wall of the body cavity (as indicated by the position of the pelvic girdle and/or anal fin, or evidence of the body cavity present as an infill). We have reinterpreted the vertebral column of *Cowralepis*, arguing that Ritchie's (2005) reconstruction inverts the dorsoventral orientation. Ritchie's sub-haemal spines are here interpreted as dorsal or caudal fin radials. This is evidenced by the fact that the series bearing these epi-spinal elements continues under the dermal shoulder armour, while the opposing series terminates at the level of the pelvic fins (based on AMF9764, Ritchie, 2005, fig. 16 A, B). This also better explains the direction of the gentle sigmoid bend seen in several specimens (Ritchie 2005, figs. 16B, 17A, C). In photographs of specimen AMF103767 (Ritchie 2005, fig. 1A-D, the orientation of the collapsed vertebral column can be observed. In the specimen showing the dorsal surface, the chordal surface the series lacking the accessory elements is observed, suggesting this was their ventral surface rather than dorsal.

0. base approximately as broad as tall, not broader than all of other median fins
1. base much longer than the height of the fin, substantially longer than any of the other dorsal fins

230. Basal plate in dorsal fin:

Friedman & Brazeau (2010: character 42).

0. absent
1. present

231. Branching radial structure articulating with dorsal fin basal plate:

0. absent
1. present

232. [DFC 137] Anal fin:

0. absent
1. present

233. Basal plate in anal fin:

Friedman & Brazeau (2010: character 42).

- 0. absent
- 1. present

234. [DFC 138] Caudal radials:

- 0. extend beyond level of body wall and deep into hypochordal lobe
- 1. radials restricted to axial lobe

235. Supraneurals in axial lobe of caudal fin:

- 0. absent
- 1. present

236. Epichordal lepidotrichia in caudal fin:

Cloutier & Ahlberg (1996: character 134), Schultze & Cumbaa (2001: character 101), Zhu & Schultze (2001: character 191), Zhu et al. (2001: character 140), Zhu & Yu (2002: character 140), Cloutier & Arratia (2004: character 173), Zhu et al. (2006: character 110), Friedman (2007: character 123), Zhu et al. (2009: character 142), Zhu et al. (2013: character 146).

- 0. absent
- 1. present

Eliminated characters:

[DFC 32] Opercular cover of branchial chamber complete or partial (0); separate gill covers and gill slits (1).

Character description from Davis et al. (2012): “Modified from Hanke and Wilson (2004): a series of gill slits (with individual covers rather than pores, as in jawless fishes), none of which is overlain partly or completely by an enlarged hyoidean gill cover, represents a possible synapomorphy of certain acanthodians and certain, but not all Chondrichthyes. Notable exceptions include the Chimaeroids, as well as *Tristychius* (Dick 1978), and the symmoriid *Falcatus* (Lund 1985), as exhibited in specimen CM 41049. With regard to the present study, species of *Acanthodes* (Heidtke 1993; Beznosov 2009) consistently exhibit a long pharyngeal region separating the pectoral girdle from the occipital region, mandibular and hyoid arches. In several *A. bronni* specimens the gill skeleton is barely disturbed. The gill arch series preserved in specimen NHM P49979 (Supplementary Figure 12 e) especially resembles conditions in *Akmonistion* and *Cladoselache*, although overlain by an impression of skin with scales (these chondrichthyan exemplars are mostly scale-free). Although the skin impression in NHM P49979 is incomplete, the simplest interpretation is of a series of gill slits and flaps. Crucially, there is no evidence of a substantial, hyoid supported, opercular cover.”

This character is deleted because it requires too much subjective judgment and is highly vulnerable to taphonomic distortions resulting from compression of material.

[DFC 73] Ethmoid region elongate with dorsoventrally deep lateral walls: absent (0); present (1).

Character description from Davis et al. (2012): “Holocephalan synapomorphy: in extant species the pre-orbital walls of the ethmoid region provide anchorage for most of the jaw adductor muscles (Didier 1995). This is a likely synapomorphy of a larger clade including non-holocephalan members of the chimaeroid total group (Stahl 1999; Grogan & Lund 2000). Although coded as uncertain in the vast majority of acanthodians, orbit and snout proportions indicate that all could be scored as ‘0’.”

This character is deleted because whether or not the ethmoid region is ‘elongate’ is highly dependent on the proportions of the braincase as a whole.

[DFC 72] Short otico-occipital region of braincase: absent (0); present (1). Schaeffer (1981); Coates & Sequeira (1998, 2001); Maisey (2001); Brazeau (2009); Davis et al. (2012).

This character is also deleted as it is highly dependent on individual braincase proportions.

[DFC 94] Process forming part or complete wall of jugular groove or canal projecting from otic capsule wall: absent (0); present (1).

Character description from Davis et al. (2012): “The anterolateral otic process of *Acanthodes* (‘Alop’, Figure 2b and d, Supplementary Figures 9 and 15) is here suggested as a possible homologue of the thickened margin and posterior postorbital process of placoderm neurocrania (Stensio 1963; Goujet 1984; Young 1980). Topographically, these processes are near-equivalents: each projects laterally from the otic wall, situated between or surrounding the jugular passage and the exit of the glossopharyngeal nerve. However, the polarity of this character is admittedly difficult to judge, relative to conditions in jawless outgroups.”

This character is deleted because the presence of a process enclosing the jugular canal is accounted for in other characters.

2. List of Taxa

Taxa included in the analyses with associated references and specimen numbers.

Taxon	References	Specimens
Galeaspida	Donoghue et al. 2000; Wang et al. 2005; Gai et al. 2011.	
Osteostraci	Denison 1947; Janvier 1985; Janvier 1996; Sansom 2009.	
<i>Acanthodes</i>	Gross 1947; Miles 1968; Miles 1973a, b; Coates 1994; Valiukevicius 1995; Davis et al. 2012.	

<i>Akmonistion</i>	Coates & Sequiera 1998; Coates et al. 1998; Coates & Sequeira 2001.	
<i>Austroptyctodus</i>	Long, 1997; Miles & Young 1977.	
<i>Bothriolepis</i>	Denison 1978; Young 1984; Young 1988.	
<i>Brachyacanthus</i>	Watson 1937; Denison 1979.	NHMUK P.6959, P.9595
<i>Brindabellaspis</i>	Young 1980; Young 1986; Burrow & Turner 1998, 1999.	
<i>Brochoadmones</i>	Bernacsek & Dineley 1977; Gagnier & Wilson 1996b; Hanke & Wilson 2006.	UALVP 41495
<i>Buchanosteus</i>	Young 1979, 1986; Young et al. 2001.	
<i>Campbellodus</i>	Miles & Young 1977; Long 1997.	
<i>Cassidiceps</i>	Gagnier & Wilson 1996a.	UALVP 32454
<i>Cheiracanthus</i>	Watson 1937; Miles 1973a; Denison 1979.	
<i>Cheirolepis</i>	Ørvig 1967; Pearson & Westoll 1979; Arratia & Cloutier 1996.	NHMUK P.62908; RSM 1877.30.5
<i>Chondrenchelys</i>	Moy-Thomas 1935; Lund 1982.	
<i>Cladodoides</i>	Gross 1937, 1938; Maisey 2005.	
<i>Cladoselache</i>	Hussakof & Bryant 1916; Woodward & White 1938; Bendix-Almgreen 1975; Schaeffer 1981, Zangerl 1981; Maisey 2007, 2008.	
<i>Climatius</i>	Watson 1937; Ørvig 1967; Miles 1973a, b.	
<i>Cobelodus</i>	Zangerl & Case 1976; Maisey 2007.	
<i>Coccosteus</i>	Stensio 1963; Miles & Westoll 1968.	
<i>Cowralepis</i>	Ritchie 2005; Carr et al. 2009; Long et al. 2009.	
<i>Culmacanthus</i>	Long, 1983; Burrow & Young 2012.	
<i>Debeerius</i>	Grogan & Lund 2000.	
<i>Dialipina</i>	Schultze 1968; Schultze and Cumbaa 2001.	
<i>Dicksonosteus</i>	Goujet 1975; Goujet 1984.	
<i>Diplacanthus</i>	Watson 1937; Miles 1973a; Gagnier 1996.	
<i>Doliodus</i>	Miller et al. 2003; Turner 2004; Maisey et al. 2009; Maisey et al. in press.	
<i>Entelognathus</i>	Zhu et al. 2013.	
<i>Eurycaraspis</i>	Liu 1991.	
<i>Eusthenopteron</i>	Jarvik 1980.	
<i>Euthacanthus</i>	Watson, 1937; Newman et al. 2011.	
<i>Gemuendina</i>	Broili 1930; Gross 1963.	
<i>Gladiobranchus</i>	Bernacsek and Dineley 1977; Hanke & Davis 2008; Newman et al. 2012.	
<i>Glyptolepis</i>	Andrews & Westoll 1970; Jarvik 1972; Cloutier & Schultze 1996; Ahlberg 1989.	
<i>Gogonasus</i>	Long et al. 1997; Long et al. 2006.	
<i>Guiyu</i>	Zhu et al. 2009.	
<i>Gyracanthides</i>	Warren et al. 2000; Turner et al. 2005.	
<i>Hamiltonichthys</i>	Maisey, 1989b.	
<i>Helodus</i>	Moy-Thomas 1936.	
<i>Homalacanthus</i>	Watson 1937; Gagnier 1996.	

<i>Howqualepis</i>	Long 1988.	AMF65495
<i>Incisoscutum</i>	Johanson & Smith 2005, Ahlberg et al. 2009.	
<i>Ischnacanthus</i>	Watson 1937; Gross 1947; Miles 1973a.	NHMUK P.7000
<i>Jagorina</i>	Stensiö 1969.	MB.f.510.5-6
<i>Kathemacanthus</i>	Gagnier & Wilson 1996a; Hanke & Wilson 2010.	
<i>Kentuckia</i>	Rayner 1951; Giles and Friedman in press.	
<i>Kujdanowiaspis</i>	Stensiö 1969; Dupret 2010.	
<i>Latviacanthus</i>	Schultze & Zidek 1982.	
<i>"Ligulalepis"</i>	Basden et al. 2000; Basden and Young 2001.	
<i>Lunaspis</i>	Heintz 1937; Gross 1961	SMF WS 10825
<i>Lupopsyrus</i>	Bernacsek & Dineley 1977; Hanke & Davis 2012.	
<i>Macropetalichthys</i>	Stensiö 1925; Gross 1935; Stensiö 1969; Denison 1978; Young, 1978.	
<i>Mesacanthus</i>	Watson 1937; Gross 1947; Miles 1973a.	
<i>Mimipiscis</i>	Gardiner & Bartram 1977; Gardiner 1984; Giles & Friedman in press.	
<i>Moythomasia</i>	Gardiner, 1984.	
<i>Obtusacanthus</i>	Hanke & Wilson 2004.	UALVP 41488
<i>Onychodus</i>	Andrews et al. 2006.	
<i>Onychoselache</i>	Dick & Maisey 1980; Coates & Gess 2007.	
<i>Orthacanthus</i>	Schaeffer 1981; Maisey 1983.	
<i>Parayunnanolepis</i>	Zhang et al. 2001; Zhu et al. 2012.	
<i>Parexus</i>	Watson 1937; Miles 1973a.	NHMUK P.130, P.38593
<i>Poracanthodes</i>	Valiukevicius 1992; Denison 1979.	
<i>Porolepis</i>	Jarvik 1972; Clement 2004.	
<i>Promesacanthus</i>	Hanke 2008.	UALVP 42652
<i>Psarolepis</i>	Zhu & Schultze 1997; Yu 1998; Zhu et al. 1999; Qu et al. 2013; Zhu et al. 2013.	
<i>Pterichthyodes</i>	Hemmings 1978.	
<i>Ptomacanthus</i>	Miles 1973a; Denison 1979; Brazeau 2009; Brazeau 2012.	
<i>Pucapampella</i>	Maisey 2001; Maisey & Anderson 2001; Janvier & Maisey 2010; Maisey & Lane 2010.	
<i>Ramirosuarezia</i>	Pradel et al. 2009.	
<i>Rhamphodopsis</i>	Miles 1967; Long 1997; Miles & Young 1977.	
<i>Romundina</i>	Goujet & Young 2004; Giles et al. 2013.	
<i>Styloichthys</i>	Zhu & Yu 2002; Zhu & Yu 2004; Friedman 2007.	
<i>Tamiobatis</i>	Schaeffer 1981; Williams 1998.	
<i>Tetanopsyrus</i>	Gagnier & Wilson 1995; Gagnier et al. 1999; Hanke et al. 2001.	UALVP 32571, 42512, 43246
<i>Tristychius</i>	Dick 1978; Coates and Gess 2007.	
<i>Vernicomacanthus waynensis</i>	Miles 1973a.	NHM P.16614, 16615, 24938a, 52441a, 52443
<i>Yunnanolepis</i>	Zhu 1996; Chang 1980; Giles et al. 2013.	

Institutional Abbreviations

AMF, Australian Museum, Sydney

MB, Museum für Naturkunde, Berlin

NHMUK, Natural History Museum, London

SMF, Senckenberg Museum, Frankfurt

UALVP, University of Alberta Laboratory of Vertebrate Palaeontology, Alberta

RSM, National Museums of Scotland, Edinburgh

Part D. Supplementary References

- Ahlberg, P. E. Paired fin skeletons and the relationships of the fossil group Porolepiformes (Osteichthyes: Sarcopterygii). *Zoological Journal of the Linnean Society* 96, 119–166 (1989).
- Ahlberg, P. E. and J. A. Clack. Lower jaws, lower tetrapods - a review based on the Devonian genus *Acanthostega*. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 88, 11–46 (1998).
- Ahlberg, P. E., & Johanson, Z. Osteolepiforms and the ancestry of tetrapods. *Nature* 395, 792–794 (1998).
- Ahlberg, P. E., E. Lukševičs and E. Mark-Kurik. A near-tetrapod from the Baltic Middle Devonian. *Palaeontology* 43, 533–548 (2000).
- Ahlberg, P., Trinajstić, K., Johanson, Z., & Long, J. Pelvic claspers confirm chondrichthyan-like internal fertilization in arthrodires. *Nature* 460, 888–889 (2009).
- Andrews, S. M., Long, J. A., Ahlberg, P. E., Barwick, R. E. & Campbell, K. S. W. The structure of the sarcopterygian *Onychodus jandemarri* n. sp. From Gogo, Western Australia: with a functional interpretation of the skeleton. *Transactions of the Royal Society of Edinburgh, Earth Sciences* 96, 197–307 (2006).
- Andrews, S. M., & Westoll, T. S. XII.—The Postcranial Skeleton of Rhipidistian Fishes Excluding *Eusthenopteron*. *Transactions of the Royal Society of Edinburgh* 68, 391–489 (1970).
- Arratia, G. & Cloutier, R. in *Devonian Fishes and Plants of Miguasha, Quebec, Canada* (eds. Schultze, H.-P. & Cloutier, R.) 165–197 (Verlag Dr. Friedrich Pfeil, Munich, 1996).
- Basden, A. M. & Young, G. C. A primitive actinopterygian neurocranium from the Early Devonian of Southeastern Australia. *Journal of Vertebrate Paleontology* 21, 754–766 (2001).
- Basden, A. M., Young, G. C., Coates, M. I. & Ritchie, A. The most primitive osteichthyan braincase? *Nature* 403, 185–188 (2000).
- Bendix-Almgreen, S. E. The paired fins and shoulder girdle in *Cladoselache*, their morphology and phyletic significance. *Colloques Internationaux du Centre National de la Recherche Scientifique* 218, 111–123 (1975).
- Bernacsek, G.M., & Dineley, D.L. New acanthodians from the Delorme Formation (Lower Devonian) of N.W.T., Canada. *Paleontographica Abteilung A* 158, 1–25 (1977).
- Blais, S. A., L. A. MacKenzie, & M. V.H. Wilson. Tooth-like scales in Early Devonian eugnathostomes and the ‘outside-in’ hypothesis for the origins of teeth in vertebrates. *Journal of Vertebrate Paleontology* 31, 1189–1199 (2011).
- Blieck, A. *Les Hétérostracés Pteraspidoformes du Silurien-Dévonien du Continent Nord-Atlantique et des blocs avoisinants: Révision systématique, phylogénie, biostratigraphie, biogéographie*. (Cahiers de Paléontologie, Section Vertébrés, Centre national de la Recherche scientifique, 1984).
- Blieck, A. & Janvier, P. in *Palaeozoic vertebrate biostratigraphy and biogeography* (ed. Long, J. A. L.) 87–103 (John Hopkins Press, 1993).
- Brazeau, M. D. The braincase and jaws of a Devonian ‘acanthodian’ and modern gnathostome origins. *Nature* 457, 305–308 (2009).
- Brazeau, M. D. A revision of the anatomy of the Early Devonian jawed vertebrate *Ptomacanthus anglicus* Miles. *Palaeontology* 55, 355–367 (2012).
- Brazeau, M. D. & Friedman, M. The characters of Palaeozoic jawed vertebrates. *Zoological Journal of the Linnean Society* 170, 779–821 (2014).
- Burrow, C. J., Newman, M. J., Davidson, R. G. & Den Blaauwen, J. L. Sclerotic plates or

- circumorbital bones in early jawed fishes? *Palaeontology* 54, 207-214 (2011).
- Burrow, C. J. & Turner, S. Devonian placoderm scales from Australia. *Journal of Vertebrate Paleontology* 18, 677-695 (1998).
- Burrow, C. J. & Turner, S. A review of placoderm scales, and their significance in placoderm phylogeny. *Journal of Vertebrate Paleontology* 19, 204-219 (1999).
- Burrow, C. J., & Young, G. C. New Information on *Culmacanthus* (Acanthodii: Diplacanthiformes) from the ?Early–Middle Devonian of Southeastern Australia. *Proceedings of the Linnean Society of New South Wales* 134 (2012).
- Carr, R. K., Johanson, Z. & Ritchie, A. The phyllolepid placoderm *Cowralepis mclachlani*: insights into the evolution of feeding mechanisms in jawed vertebrates. *Journal of Morphology* 270, 775-804 (2009).
- Cherkesova, S. V. Lower and Middle Devonian marine deposits of the Soviet Arctic and the correlation with Arctic Canada. CSPG Special Publications, 669-679 (1988).
- Clement, G. Nouvelles données anatomiques et morphologie générale des “Porolepididae” (Dipnomorpha, Sarcopterygii). *Revue de Paléobiologie, Genève* Volume spéciale 9, 193-211 (2004).
- Cloutier, R., & Ahlberg, P. E. in *Interrelationships of Fishes* (eds Stiassny, M. L. J., Parenti, L. R., & Johnson, G. D.) 445–479. (Academic Press, 1996).
- Cloutier, R., & Arratia, G. in *Recent Advances in the Origin and Early Radiation of Vertebrates*. (eds Arratia, G., Wilson, M. V. H., & Cloutier, R.) 217–270 (Freidrich Pfeil, 2004).
- Cloutier, R., & Schultze, H.-P., in *Devonian Fishes and Plants of Miguashaia, Quebec, Canada*. (eds. Schultze, H.-P., & Cloutier, R.) 248–270 (Friedrich Pfeil, 1996).
- Coates, M. I. The origin of vertebrate limbs. *Development* Supplement, 169-180 (1994).
- Coates, M. I. Endocranial preservation of a Carboniferous actinopterygian from Lancashire, UK, and the interrelationships of primitive actinopterygians. *Philosophical Transactions of the Royal Society of London: B* 354, 435–462 (1999).
- Coates, M. I., & Gess, R. W. A new reconstruction of *Onychoselache traquairi*, comments on early chondrichthyan pectoral girdles and hybodontiform phylogeny. *Palaeontology* 50, 1421-1446 (2007).
- Coates, M. I., Sansom, I. J. & Smith, M. M. Spines and tissues of ancient sharks. *Nature* 396, 729-730 (1998).
- Coates, M. I. & Sequeira, S. E. K. The braincase of a primitive shark. *Transactions of the Royal Society of Edinburgh (Earth Sci.)* 89, 63–85 (1998).
- Coates, M. I. & Sequeira, S. E. K. A new stethacanthid chondrichthyan from the Lower Carboniferous of Bearsden, Scotland. *Journal of Vertebrate Paleontology* 21, 754–766 (2001).
- Coates, M.I. & Sequeria, S. E. K. in *Major Events in Early Vertebrate Evolution* (ed. Ahlberg, P. E.) 241–262 (Taylor and Francis, 2001a).
- Daeschler, E. B., Shubin, N. H., & Jenkins, F. A. A Devonian tetrapod-like fish and the evolution of the tetrapod body plan. *Nature* 440, 757-763 (2006).
- Davis, S. P., Finarelli, J. A. & Coates, M. I. *Acanthodes* and shark-like conditions in the last common ancestor of modern gnathostomes. *Nature* 486, 247-250 (2012).
- Dennis, K. & Miles, R. S. A pachyosteomorph arthrodire from Gogo, Western Australia. *Zoological Journal of the Linnean Society* 73, 213–258 (1981).
- Dietze, K. A revision of paramblypterid and amblypterid actinopterygians from Upper Carboniferous–Lower Permian lacustrine deposits of Central Europe. *Palaeontology* 43, 927-966 (2000).

- Denison, R. H. The exoskeleton of *Tremataspis*. *American Journal of Science* 245, 337-365 (1947).
- Denison, R. in *Handbook of Paleoichthyology* Vol. 2 (ed. Schultze, H.-P.) (Gustav Fischer Verlag, Stuttgart, 1978).
- Denison, R. in *Handbook of Paleoichthyology* Vol. 5 (ed. Schultze, H.-P.) (Gustav Fischer Verlag, Stuttgart, 1979).
- Dick, J. R. R. On the Carboniferous shark *Tristychius arcuatus* Agassiz from Scotland. *Transactions of the Royal Society of Edinburgh* 70, 63–109 (1978).
- Dick, J. R. F., & Maisey, J. G. The Scottish Lower Carboniferous shark *Onychoselache traquairi*. *Palaeontology* 23, 363-374 (1980).
- Donoghue, P. C. J., Forey, P. L., & Aldridge, R. J. Conodont affinity and chordate phylogeny. *Biological Reviews* 75, 191–251 (2000).
- Dupret, V. Revision of the genus *Kujdanowiaspis* Stensiö, 1942 (Placodermi, Arthrodira, "Actinolepida") from the Lower Devonian of Podolia (Ukraine). *Geodiversitas* 32, 5–63 (2010).
- Elliott, D. K & Carr, R. K. A new species of *Bryantolepis* Camp, Welles and Green, 1949 (Placodermi, Arthrodira) from the Early Devonian Water Canyon formation of northern Utah and southern Idaho, with comments on the endocranium. *Kirtlandia* 57, 22–35 (2010).
- Forey, P. *History of the coelacanth fishes*. Springer (1998).
- Friedman, M. *Styloichthys* as the oldest coelacanth: implications for early osteichthyan interrelationships. *Journal of Systematic Palaeontology* 5, 289–343 (2007).
- Friedman, M., & H. Blom. A new actinopterygian from the Famennian of East Greenland and the interrelationships of Devonian ray-finned fishes. *Journal of Paleontology* 80, 1186–1204 (2006).
- Friedman, M. & Brazeau, M. A reappraisal of the origin and basal radiation of the Osteichthyes. *Journal of Vertebrate Paleontology* 30, 36–56 (2010).
- Gai, Z., Donoghue, P. C. J., Zhu, M., Janvier, P. & Stampanoni, M. Fossil jawless fish from China foreshadows early jawed vertebrate anatomy. *Nature* 476, 324-367 (2011).
- Gagnier, P. Y. in *Devonian Fishes and Plants of Miguasha, Quebec, Canada*. (eds Schultze, H. P. & Cloutier, R.) 149–163 (Freidrich Pfeil, 1996).
- Gagnier, P.-Y., Hanke, G. F. & Wilson, M. V. H. *Tetanopsyrus lindoei* gen. et sp. nov., an Early Devonian acanthodian from the Northwest Territories, Canada. *Acta Geologica Polonica* 49, 81- 96 (1999).
- Gagnier, P.-Y. & Wilson, M. V. H. New evidences on jaw bones and jaw articulations in acanthodians. *Geobios* 19 (1995).
- Gagnier, P.-Y. & Wilson, M. V. H. Early Devonian acanthodians from northern Canada. *Palaeontology* 39, 241–258 (1996a).
- Gagnier, P. -Y. & Wilson, M. V. H. An unusual acanthodian from Northern Canada: revision of *Brochoadmones milesi*. *Modern Geology* 20, 235-251 (1996b).
- Gardiner, B. G. The relationships of the palaeoniscoid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia. *Bulletin of the British Museum (Natural History)*. Geology 37, 173–428 (1984).
- Gardiner, B. G. & Bartram, A. W. H. in *Problems in Vertebrate Evolution* (eds Andrews, S. M., Miles, R. S., Walker & A. D.) 227-245 (Linnean Symposium Series, London, 1977).
- Gardiner, B. G., & B. Schaeffer. Interrelationships of lower actinopterygian fishes. *Zoological Journal of the Linnean Society* 97, 135–187 (1989).

- Gardiner, B. G., Schaeffer, B., & Massare, J. A. A review of the lower actinopterygian phylogeny. *Zoological Journal of the Linnean Society* 144, 511–525 (2005).
- Giles, S., & Friedman, M. Virtual reconstruction of endocast anatomy in early ray-finned fishes (Osteichthyes: Actinopterygii). *Journal of Paleontology* (accepted).
- Giles, S., Rücklin, M., & Donoghue, P. C. J. Histology of “placoderm” dermal skeletons: Implications for the nature of the ancestral gnathostome. *Journal of Morphology* 274, 627–644 (2013).
- Goujet, D. *Dicksonosteus*, un nouvel arthrodire du Dévonien du Spitsberg. Remarques sur le squelette viscéral des Dolichothoraci. *Colloques Internationaux du Centre National de la Recherche Scientifique* 218, 81–99 (1975).
- Goujet, D. *Les Poissons Placodermes du Spitsberg* (Cahiers de Paléontologie, Section Vertébrés, Centre national de la Recherche scientifique, 1984).
- Goujet, D. Placoderm interrelationships: a new interpretation, with a short review of placoderm classifications. *Proceedings of the Linnean Society of New South Wales* 107, 211–244 (1984b).
- Goujet, D. in *Major Events in Early Vertebrate Evolution* (ed. Ahlberg, P. E.) 209–222 (Taylor and Francis, 2001).
- Goujet D. & Young G. C. in *Recent Advances in the Origin and Early Radiation of Vertebrates*, (eds Arratia, G., Wilson, M. V. H. & Cloutier, R.) 109–26 (Friedrich Pfeil, 2004).
- Gradstein, F. M., Ogg, J. G., & Schmitz, M. (Eds.). *The Geologic Time Scale 2012*, 2-volume set. (Elsevier, 2012).
- Grogan, E. D. & Lund, R. *Debeerius ellefseni* (Fam. Nov., Gen. Nov., Sped. Nov.) an Autodiastylic Chondrichthyan From the Mississippian Bear Gulch Limestone of Montana (USA), the Relationships of the Chondrichthyes, and Comments on Gnathostome Evolution. *Journal of Morphology* 243, 219–245 (2000).
- Gross, W. Histologischen Studien am Aussenskelett fossiler Agnathen und Fische. *Palaeontographica Abteilung A* 83, 1–60 (1935).
- Gross, W. Das Kopfskelett von *Cladodus wildungensis* Jaekel; 1. Teil. Endocranium und Palatoquadratum. *Senckenbergiana* 19, 80–107 (1937).
- Gross, W. Das Kopfskelett von *Cladodus wildungensis* Jaekel; 2. Teil. Der Kieferbogen. Anhang: *Protractodus vetustus* Jaekel. *Senckenbergiana* 20, 123–145 (1938).
- Gross, W. Die Agnathen und Acanthodier des obersilurischen Beyrichienkalks. *Palaeontographica Abteilung A* 96, 91–158 (1947).
- Gross, W. *Lunaspis broilii* und *Lunaspis heroldi* aus dem Hunsrückschiefer (Unterdevons, Rheinland). *Notizblatt Hessisches Landesamtes für Bodenforschung zu Wiesbaden* 89, 17–43 (1961).
- Gross W. *Gemuendina stuertzi* Traquair. Neuuntersuchung. *Notizblatt Hessisches Landesamtes für Bodenforschung zu Wiesbaden* 91, 36–73 (1963).
- Hanke G. F. *Promesacanthus eppleri* n. gen., n. sp., a mesacanthid (Acanthodii, Acanthodiformes) from the Lower Devonian of northern Canada. *Geodiversitas* 30, 287–302 (2008).
- Hanke, G. F. & Davis, S. P. Redescription of the acanthodian *Gladiobranchus probaton* Bernacsek & Dineley, 1977, and comments on diplacanthid relationships. *Geodiversitas* 30, 303–330 (2008).
- Hanke, G. F., & Davis, S. P. A re-examination of *Lupopsyrus pygmaeus* Bernacsek & Dineley, 1977 (Pisces, Acanthodii). *Geodiversitas* 34, 469–487 (2012).
- Hanke, G. F., Davis, S. P. & Wilson, M. V. H. A new species of the acanthodian genus *Tetanopsyrus* from Northern Canada, with comments on related taxa. *Journal of*

- Vertebrate Paleontology* 21, 740-753 (2001).
- Hanke, G. F., & Wilson, M. V. H. in *Recent Advances in the Origin and Early Radiation of Vertebrates*. (eds Arratia, G., Wilson, M. V. H., & Cloutier, R.) 189–216 (Freidrich Pfeil, 2004).
- Hanke, G. F. & Wilson, M. V. H. Anatomy of the Early Devonian Acanthodian *Brochoadmones milesi* based on nearly complete body fossils, with comments on the evolution and development of paired fins. *Journal of Vertebrate Paleontology* 26, 526-537 (2006).
- Heintz, A. Die Downtonischen und Devonischen Vertebraten von Spitzbergen VI. *Lunaspis*-arten aus dem Devon Spitzbergens. *Skrifter om Svalbad og Ishavet* 22, 1–81 (1937).
- Hemmings, S. K. A monograph of the Old Red Sandstone antiarchs of Scotland: *Pterichthyodes* and *Microbrachius*. *Palaeontographical Society [Monographs]* 131, 1-64 (1973).
- Holmgren, N. Studies on the head of fishes. Embryological, morphological, and phylogenetical researches. Part I: Development of the skull in sharks and rays. *Acta Zoologica* 21, 51-266 (1940).
- Hussakof, L. & Bryant, W. L. Catalog of the fossil fishes in the Museum of Buffalo Society of Natural Sciences. *Bulletin of the Buffalo Society of Natural Sciences* 12, 5-178. (1918).
- Janvier, P. *Les Céphalaspides du Spitzberg. Anatomie, phylogénie et systématique des Ostéostracés siluro-dévonien*. Révision des Ostéostracés de la Formation de Wood Bay (Dévonien inférieur du Spitzberg) (Cahiers de Paléontologie, Section Vertèbres, Centre National de la Recherche Scientifique, 1985).
- Janvier, P. *Early Vertebrates* (Oxford University Press, 1996).
- Janvier, P., & Maisey, J. G. in *Morphology, Phylogeny and Biogeography of Fossil Fishes* (eds Elliott, D. K., Maisey, J. G., Yu, X. & Miao, D) 431-459 (Verlag Dr. Friedrich Pfeil, Munich, 2010).
- Jarvik, E. Middle and Upper Devonian Porolepiformes from East Greenland with special reference to *Glyptolepis groenlandica* n. sp. *Meddelelser om Grønland* 187, 1-307 (1972).
- Jarvik, E. *Basic Structure and Evolution of Vertebrates* (Academic, 1980).
- Johanson Z, Smith MM. Origin and evolution of gnathostome dentitions: a question of teeth and pharyngeal denticles in placoderms. *Biological Reviews* 80, 303–45 (2005).
- Karatajute-Talimaa, V. N. in *Stratigrafiya i fauna nijnedevonskikh otlojenniy Taryeiskogo oprnogo razreza (Taimyr)*. [Stratigraphy and fauna of Lower Devonian deposits of the Taraya key section (central Taimyr)] (eds Tcherkessova, S. V., Karatajute-Talimaa, V. N., & Matukhin, R. G.) 100-116. (Nedra, 1994).
- Krylova, A. K., Malitch, N. S., Menner, V. V., Obrutchev, D. V., Fradkin, G. S. in *International Symposium on the Devonian system Vol 1* (ed. Oswald, D. H.) 473-482 (Calgary, 1967).
- Lauder, G. V., and Liem, K. F. The evolution and interrelationships of the actinopterygian fishes. *Bulletin of the Museum of Comparative Zoology, Harvard University* 150, 95–197 (1983).
- Liu, Y. H. On a new petalichthyid, *Eurycaraspis incilis* gen. et sp. nov., from the middle Devonian of Zhanyi, Yunnan. *Early Vertebrates and Related Problems of Evolutionary Biology*. Science Press, Beijing, 139-177 (1991).
- Long, J. A. A new diplacanthoid acanthodian from the Late Devonian of Victoria. *Memoirs*

- of the Association of Australasian Palaeontologists 1, 51-65 (1983).
- Long, J. A. in *Devonian and Carboniferous fish studies*. (ed. Jell, P. A.) 1-64 (Memoir 7, Association of Australian Palaeontologists, Sydney, 1988).
- Long, J. A. Ptyctodontid fishes (Vertebrata, Placodermi) from the Late Devonian Gogo Formation, Western Australia, with a revision of the European genus *Ctenurella* Ørvig, 1960. *Geodiversitas* 19, 515–555. (1997).
- Long, J. A., Barwick, R. E., & Campbell. Osteology and functional morphology of the osteolepiform fish *Gogonassus andrewsae* Long 1995, from the Upper Devonian Gogo Formation, Western Australia. *Records of the Western Australian Museum Supplement* 53, 1-89 (1997).
- Long, J. A., Young, G. C., Holland, T., Senden, T. J. & Fitzgerald, E. M. G. An exceptional Devonian fish from Australia sheds light on tetrapod origins. *Nature* 444, 199-202 (2006).
- Long, J. A., Trinajstić, K. M., Young, G., Senden T. Devonian arthrodire embryos and the origin of internal fertilization in vertebrates. *Nature* 457, 1124-1127 (2009).
- Lund, R. *Harpagofututor volsellorhinus* new genus and species (Chondrichthyes, Chondrenchelyiformes) from the Namurian Bear Gulch Limestone, *Chondrenchelys problematica* Traquair (Visean), and their sexual dimorphism. *Journal of Paleontology* 56, 938–958 (1982).
- Lund, R., Poplin, C., & McCarthy, K. Preliminary analysis of the interrelationships of some paleozoic actinopterygii. *Geobios* 28, 215-220 (1995).
- Lund, R. The new actinopterygian order Guildayichthyiformes from the Lower Carboniferous of Montana (USA). *Geodiversitas* 22, 171-206 (2000).
- Lund, R., & Poplin, C. Cladistic analysis of the relationships of the tarrasiids (Lower Carboniferous Actinopterygians). *Journal of Vertebrate Paleontology* 22, 480-486 (2002).
- Maisey, J. G. Cranial anatomy of *Hybodus basanus* Egerton from the Lower Cretaceous of England. *American Museum Novitates* 2758, 1–64 (1983).
- Maisey, J. G. Heads and Tails: a chordate phylogeny. *Cladistics* 2, 201–256 (1986).
- Maisey, J. G. *Hamiltonichthys mapei* g. & sp. nov. (Chondrichthyes; Elasmobranchii), from the Upper Pennsylvanian of Kansas. *American Museum Novitates* 2931, 1-42 (1989).
- Maisey, J. G. in *Major Events in Early Vertebrate Evolution* (ed. Ahlberg, P. E.) 263–288 (Taylor and Francis, 2001).
- Maisey, J. G. Braincase of the Upper Devonian shark *Cladodoides wildungensis* (Chondrichthyes, Elasmobranchii), with observations on the braincase in early chondrichthyans. *Bulletin of the British Museum (Natural History)* 288, 1–103 (2005).
- Maisey, J. G. The braincase in Paleozoic symmoriiform and cladoselachian sharks. *Bulletin of the British Museum (Natural History)* 307, 1–122 (2007).
- Maisey, J. 2008. Cladoselache: an iconic Devonian shark. *Journal of Vertebrate Paleontology* Vol. 28 (Supplement to No. 3): 111A.
- Maisey, J. G. & Anderson, M. E. A primitive chondrichthyan braincase from the Early Devonian of South Africa. *Journal of Vertebrate Paleontology* 21, 702-713 (2001).
- Maisey, J. G. & Lane, J. A. Labyrinth morphology and the evolution of low-frequency phonoreception in elasmobranchs. *Comptes Rendus Palevol* 9, 289-309. (2010)
- Maisey, J. G., Miller, R. & Turner, S. The braincase of the chondrichthyan *Doliodus* from the Lower Devonian Campbellton Formation of New Brunswick, Canada. *Acta Zoologica* 90 (supplement 1), 109-122 (2009)

- Maisey, J. G., Turner, S., Naylor, G. J.P. and Miller, R. F. Dental patterning in the earliest sharks: Implications for tooth evolution. *Journal of Morphology*. (In press/available online.)
- Mark-Kurik, E. (1974). Discovery of new Devonian fish localities in the Soviet Arctic. *Eesti NSV Teaduste Akadeemia Toimetised, Geoloogia* 23: 332-335.
- Mark-Kurik, E. in *Stratigrafiya I fauna nijnedevonskikh otlojenniy Taryeiskogo oprnogo razreza (Taimyr)*. [Stratigraphy and fauna of Lower Devonian deposits of the Taraya key section (central Taimyr)] (eds Tcherkessova, S. V., Karatajute-Talimaa, V. N., & Matukhin, R. G.) 123-131. (Nedra, 1994).
- Miles, R. S. Observations on the ptyctodont fish, *Rhamphodopsis* Watson. *Journal of the Linnean Society of London, Zoology* 47, 99-120 (1967).
- Miles, R. S. in *Current problems of lower vertebrate phylogeny*. (ed. T. Ørvig) 109-127 (Almqvist & Wiksell, Stockholm, 1968).
- Miles, R. S. Articulated acanthodian fishes from the Old Red Sandstone of England, with a review of the structure and evolution of the acanthodian shoulder- girdle. *Bulletin of the British Museum Natural History (Geology)* 24, 111-213 (1973a).
- Miles, R. S. in *Interrelationships of Fishes* (eds Greenwood, P. H., Miles, R. S. & Patterson, C.) 63-103 (Academic, 1973b).
- Miles, R. S. Dipnoan (lungfish) skulls and the relationships of the group: a study based on new species from the Devonian of Australia. *Zoological Journal of the Linnean Society* 61, 1-328 (1977).
- Miles, R. S. & Dennis, K. A primitive eubrachythoracid arthrodire from Gogo, Western Australia. *Zoological Journal of the Linnean Society* 66, 31-62 (1979).
- Miles, R. S. & Westoll, T. S. The placoderm fish *Coccosteus cuspidatus* Miller ex Agassiz from the Middle Old Red Sandstone of Scotland. *Transactions of the Royal Society of Edinburgh* 67, 373-476 (1968).
- Miles, R. S. & Young, G. C. in *Problems in Vertebrate Evolution*. (eds Andrews, S. M., Miles, R. S., Walker & A. D.) 123-198 (Linnean Symposium Series, London, 1977).
- Miller, R. F., Cloutier, R. & Turner, S. The oldest articulated chondrichthyan from the Early Devonian period. *Nature* 425, 501-504 (2003).
- Moy-Thomas, J. A. On the structure and affinities of the Carboniferous cochlodont *Helodus simplex*. *Geological Magazine* 73, 488-503 (1936).
- Moy-Thomas, J. A. The early evolution and relationships of the elasmobranchs. *Biological Reviews* 14, 1-26 (1939).
- Newman, M. J., Davidson, R. G., Den Blaauwen, J. L., & Burrow, C. J. The Early Devonian Acanthodian *Euthacanthus gracilis* from the Midland Valley of Scotland. *Scottish Journal of Geology* 47, 101-111 (2011).
- Newman, M. J., Davidson, R. G., Blaauwen, J. L. D., & Burrow, C. J. The Early Devonian Acanthodian *Uraniacanthus curtus* (Powrie, 1870) n. comb. from the Midland Valley of Scotland. *Geodiversitas* 34, 739-759 (2012).
- Novitskaya, L. I. Subdivision of the Kureyka suite based on amphiaspid (Agnatha) assemblages. *International Geology Review* 19, 1077-1084 (1977).
- Novitskaya, L. I. in *Stratigrafiya I fauna nijnedevonskikh otlojenniy Taryeiskogo oprnogo razreza (Taimyr)*. [Stratigraphy and fauna of Lower Devonian deposits of the Taraya key section (central Taimyr)] (eds Tcherkessova, S. V., Karatajute-Talimaa, V. N., & Matukhin, R. G.) 116-123. (Nedra, 1994).
- Obruchev, D. V., Cherkesova, S. V., Menner, V. V., Novitskaya, L. I. & Patrunov, D. K. in *Stratigrafiya nizhnego i srednego devona. Trudy 3-go mezhdunarodnogo simpoziuma po granitse silura i devona i stratigrafiya nizhnego i srednego devona*

- [*Stratigraphy of the Lower and Middle Devonian. Transactions of the 3rd International Symposium on the Silurian and Devonian Boundary and Stratigraphy of the Lower and Middle Devonian*] (Ed. Nalivkin, D. V.) 198-204. (Nauka, 1973).
- Obruchev, D. V. 1964. Subclass Heterostraci (pteraspides). 45- 82 In Orlov, J. A. (ed) Fundamentals of Paleontology XI: Agnatha, Pisces. Nauka, Moscow. [in Russian]
- Olive, S., Goujet, D., Lelièvre, H. & Janjou, D. A new Placoderm fish (Acanthothoraci) from the Early Devonian Jauf Formation (Saudi Arabia). *Geodiversitas* 33, 393–409 (2011).
- Ørvig, T. In *Structural and Chemical Organisation of Teeth* (ed. Miles, A. E. W.), 45–110. (Academic Press, 1967).
- Patterson, C. Morphology and interrelationships of primitive actinopterygian fishes. *American Zoologist* 22, 241-259 (1982).
- Pearson, D. M. & Westoll, T. S. The Devonian actinopterygian *Cheirolepis* Agassiz. *Transactions of the Royal Society of Edinburgh* 70, 337–399 (1979).
- Poplin, C., & Lund, R. Two new deep-bodied palaeoniscoid actinopterygians from Bear Gulch (Montana, USA, Lower Carboniferous). *Journal of Vertebrate Paleontology* 20, 428-449 (2000).
- Pradel, A., Maisey, J., Tafforeau, P., & Janvier, P. An enigmatic vertebrate skull from the Middle Devonian of Bolivia. *Acta Zoologica* 90, 123-133 (2009).
- Pradel, A., Maisey, J., Tafforeau, P., Mapes, R. H., & Mallatt, J. A Palaeozoic shark with osteichthyan-like branchial arches. *Nature* 509, 608-611 (2014).
- Pradel, A., Tafforeau, P., Maisey, J. G., & Janvier, P. A new Paleozoic Symmoriiformes (chondrichthyes) from the Late Carboniferous of Kansas (USA) and cladistic analysis of early chondrichthyans. *PloS one* 6, e24938 (2011).
- Qu, Q., Zhu, M., & Wang, W. Scales and Dermal Skeletal Histology of an Early Bony Fish *Psarolepis romeri* and Their Bearing on the Evolution of Rhombic Scales and Hard Tissues. *PloS one* 8, e61485 (2013).
- Rayner, D. H. III.—On the Cranial Structure of an Early Palæoniscid, Kentuckia, gen. nov. *Transactions of the Royal Society of Edinburgh* 62, 53-83 (1951).
- Ritchie, A. *Cowralepis*, a new genus of phyllolepid fish (Pisces, Placodermi) from the late Middle Devonian of New South Wales, Australia. *Proceedings of the Linnean Society of New South Wales* 126, 215–259 (2005).
- Rosen, D. E., Forey, P. L., Gardiner, B. G., & Patterson, C. Lungfishes, tetrapods, paleontology, and plesiomorphy. *Bulletin of the American Museum of Natural History* 167, 159–276 (1981).
- Sansom, R. Phylogeny, classification and character polarity of the Osteostraci (Vertebrata). *Journal of Systematic Palaeontology* 7, 95-115 (2009).
- Schaeffer, B. The xenacanth shark neurocranium, with comments on elasmobranch monophyly. *Bulletin of the American Museum of Natural History* 169, 1–66 (1981).
- Schultze, H. P. Palaeoniscoidea-Schuppen aus dem Unterdevon Australiens und Kanadas und aus dem Mitteldevon Spitzbergens Bulletin of the British Museum (Natural History) 16, 343-376 (1968).
- Schultze, H. P. Ausgangsform und Entwicklung der rhombischen Schuppen der Osteichthyes (Pisces). *Paläontologische Zeitschrift* 51, 152-168 (1977).
- Schultze, H. P. in *Fossil Fishes as Living Animals* (ed. Mark-Kurik, E) 233-242 (Academia, Tallinn, 1992).
- Schultze, H. -P. & Cumbaa, S. L. in *Major Events in Early Vertebrate Evolution* (ed. Ahlberg, P. E.) 315–332 (Taylor and Francis, 2001).
- Schultze, H.-P. & J. Zidek. Ein primitiver acanthodier (Pisces) aus dem Unterdevon

- Lettlands. *Paläontologische Zeitschrift* 56, 95-105 (1982).
- Stensiö, E. A. On the head of the macropetalichthyids, with certain remarks on the head of the other arthrodires. *Publications of the Field Museum of Natural History (Geology)* 4, 87-197 (1925).
- Stensiö, E. A. Anatomical studies on the arthrodiran head (Part I). *Kungliga Svenska Vetenskaps-Akademiens Handlingar Series 4.*, 8 (1963).
- Stensiö, E. in *Traité de Paléontologie* (ed. Piveteau, J.) 71-692 (Masson, Paris, 1969).
- Swofford, D. L. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.
- Taverne, L. *Osorioichthys marginis*. Paléonisciforme du Famennien de Belgique, et la phylogénie des Actinoptérygiens dévoniens (Pisces). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* 67, 57-78 (1997).
- Trinajstić, K., Long, J. A., Johanson, Z., Young, G., & Senden, T. New morphological information on the ptyctodontid fishes (Placodermi, Ptyctodontida) from Western Australia. *Journal of Vertebrate Paleontology*, 32, 757-780 (2012).
- Turner, S. in *Recent Advances in the Origin and Early Radiation of Vertebrates*. (eds Arratia, G., Wilson, M. V. H., & Cloutier, R.) 65-94 (Freidrich Pfeil, 2004).
- Turner, S., Burrow, C. J., & Warren, A. *Gyracanthides hawkinsi* sp. nov. (Acanthodii, Gyracanthidae) from the Lower Carboniferous of Queensland, Australia, with a review of gyracanthid taxa. *Palaeontology* 48, 963-1006 (2005).
- Valiukevičius, J. in *Fossil Fishes as Living Animals* (ed. Mark-Kurik, E.) 193-213 (Academy of Sciences of Estonia, Tallinn, 1992).
- Valiukevičius, J. in *Stratigrafiya I fauna nijnedevonskikh otlojenniy Taryeiskogo oprnogo razreza (Taimyr)*. [*Stratigraphy and fauna of Lower Devonian deposits of the Taraya key section (central Taimyr)*] (eds Tcherkessova, S. V., Karatajute-Talimaa, V. N., & Matukhin, R. G.) 131-197. (Nedra, 1994).
- Valiukevičius, J. Acanthodian histology: Some significant aspects in taxonomical and phylogenetical research. *Geobios* 28, 157-159 (1995).
- Wang, N.-Z., Donoghue, P. C. J., Smith, M. M. & Sansom, I. J. Histology of the galeaspid dermoskeleton and endoskeleton, and the origin and early evolution of the vertebrate cranial endoskeleton. *Journal of Vertebrate Paleontology* 25, 745-756 (2005).
- Warren, A., Currie, B. P., Burrow, C., & Turner, S. A redescription and reinterpretation of *Gyracanthides murrayi* Woodward 1906 (Acanthodii, Gyracanthidae) from the Lower Carboniferous of the Mansfield Basin, Victoria, Australia. *Journal of Vertebrate Paleontology* 20, 225-242 (2000).
- Watson, D. M. S. The acanthodian fishes. *Philosophical Transactions of the Royal Society of London B* 228, 49-146 (1937).
- Williams, M. E. A new specimen of *Tamiobatis vetustus* (Chondrichthyes, Ctenacanthoidea) from the Late Devonian Cleveland Shale of Ohio. *Journal of Vertebrate Paleontology* 18, 251-260 (1998).
- Woodward, A. S. & White, E. I. The dermal tubercles of the Upper Devonian shark, *Cladoselache*. *Annals and Magazine of Natural History* 11, 367-368 (1938).
- Young, G. C. A new Early Devonian petalichthyid fish from the Taemas/Wee Jasper region of New South Wales. *Alcheringa* 2, 103-116 (1978).
- Young, G. C. New information on the structure and relationships of *Buchanosteus* (Placodermi: Euarthrodira) from the Early Devonian of New South Wales. *Zoological Journal of the Linnean Society* 66, 309-352 (1979).
- Young, G. C. A new early Devonian placoderm from New South Wales, Australia, with a

- discussion of placoderm phylogeny. *Palaeontographica A* 167, 10–76 (1980).
- Young, G. C. The relationships of placoderm fishes. *Zoological Journal of the Linnean Society* 88, 1–57 (1986).
- Young, G. C. Antiarchs (placoderm fishes) from the Devonian Aztec sandstone, southern Victorian Land, Antarctica. *Palaeontographica A* 202, 1–125 (1988).
- Young, G. C., Lelièvre, H. & Goujet, D. Primitive jaw structure in an articulated brachythoracid arthrodire (placoderm fish; Early Devonian) from southeastern Australia. *Journal of Vertebrate Paleontology* 21, 670–678 (2001).
- Yu, X. A new porolepiform-like fish, *Psarolepis romeri*, gen. et sp. nov. (Sarcopterygii, Osteichthyes) from the Lower Devonian of Yunnan, China. *Journal of Vertebrate Paleontology* 18, 261–264 (1998).
- Zangerl, R. *Handbook of Paleichthyology* (ed. Schultze, H.-P.) (Gustav Fischer Verlag, Stuttgart, 1981).
- Zangerl, R. & Case, G. R. *Cobelodus aculeatus* (Cope), an anacanthous shark from Pennsylvanian black shales of North America. *Palaeontographica A* 154, 107–157 (1976).
- Zhang, G.-R., Wang, J.-Q. & Wang, N.-Z. The structure of pectoral fin and tail of Yunnanolepidoidei, with a discussion of the pectoral fin of chuchinolepids. *Vertebrata Palasiatica* 39, 1–13 (2001).
- Zhang, M.-M. Preliminary notes on a Lower Devonian antiarch from Yunnan, China. *Vertebrata Palasiatica* 18, 179–190 (1980).
- Zhu, M. The phylogeny of antiarcha (Placodermi, Pisces), with the description of Early Devonian antiarchs from Qujing, Yunnan, China. *Bulletin du Muséum national d'histoire naturelle* 18, 233–347 (1996).
- Zhu, M., & Ahlberg, P. E. (2004). The origin of the internal nostril of tetrapods. *Nature* 432, 94–97.
- Zhu, M. & Schultze, H. P. The oldest sarcopterygian fish. *Lethaia* 30, 293–304 (1997).
- Zhu, M. & Schultze, H. P. in *Major Events in Early Vertebrate Evolution (Palaeontology, phylogeny, genetics, and development)*. (ed. Ahlberg, P. E.) 289–314 (Taylor and Francis, 2001).
- Zhu, M & Yu, X. A primitive fish close to the common ancestor of tetrapods and lungfish. *Nature* 418, 767–770 (2002).
- Zhu, M., Yu, X. & Ahlberg, P. E. A primitive sarcopterygian fish with an eyestalk. *Nature* 410, 81–84 (2001).
- Zhu, M., Yu, X., Ahlberg, P. E., Choo, B., Lu, J., Qiao, T., Qu, Q., Zhao, W., Jia, L., Blom, H. & Zhu, Y. A. (2013). A Silurian placoderm with osteichthyan-like marginal jaw bones. *Nature*, 502, 188–193.
- Zhu, M., Yu, X., Choo, B., Wang, J.-Q. & Jia, L.-T. An antiarch placoderm shows that pelvic girdles arose at the root of jawed vertebrates. *Biology Letters* 8, 453–456 (2012).
- Zhu, M., Yu, X. & Janvier, P. A primitive fossil fish sheds light on the origin of bony fishes. *Nature* 397, 607–610 (1999).
- Zhu, M., Zhao, W., Jia, L., Lu, J., Qiao, T. & Qu, Q. The oldest articulated osteichthyan reveals a mosaic of gnathostome characters. *Nature* 458, 469–474 (2009).
- Zhu, M., Yu, X., Wang, W., Zhao, W., & Jia, L. A primitive fish provides key characters bearing on deep osteichthyan phylogeny. *Nature* 441, 77–80 (2006).